Can the brain be divided into a sensory and a motor part?

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Motor-sensory feedback and geometry of visual space: an attempted replication

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Abstract: This study involved a partial replication of an experiment performed by Held & Rekosh (1963) on the relation between prism-induced changes in visuomotor feedback and shifts in the perception of straightness. The Held & Rekosh study is important because its methodology makes it possible to clearly separate changes in perception due to visuomotor feedback from those due to other perceptual factors. Thus it bears unambiguously on the hypothesis that the neurological processing of sensory input is dependent on the organization of motor activity. The present paper consists of a brief review of theory and experiment on sensorimotor phenomena in perception, followed by a detailed consideration of the Held & Rekosh study and the present replication. For greater effectiveness, Held & Rekosh should have used base-up and base-down prism orientations rather than the base-left and base-right orientations that they employed, but in any case our replication yielded negative results for both base-up and base-right. It is concluded that, given the minimally effective prism orientation and the attentional loads characterizing the Held & Rekosh study, there is need for further experimentation with these two variables. A more drastic suggestion is that there may be a need to confront anew the evidence for sensorimotor processes in perception.

Keywords: afference; attention; feedback; geometry of visual space; motor activity; plasticity; prism-induced transformations; sensorimotor integration; visual rearrangement

The present study is in part a replication of an experiment published under the same title by Held and Rekosh (1963). A replication was called for in view of (1) the theoretical importance of the research and the novel method that formed the basis of that study, (2) its exceptionally strong and uniform findings, which stand in some contrast to what is usually obtained in this type of research, and (3) the authors' failure to pay specific attention to certain theoretical and methodological problems.

Theoretical background

The Held & Rekosh study was designed to show that motor and visual-sensory processes interact to produce percepts. As pointed out by Gyr (1972, 1975), this approach to perception may be contrasted with another important approach in psychology (e.g. Gibson, 1966), which has been concerned chiefly with the detailed analysis of external variables in the visual array (such as texture gradients, motion parallax, etc.) for predicting specific perceptual events. Unlike Held and his coworkers, researchers from this latter school of thought generally have not been interested in studying whether, with the visual array constant, nonvisual events such as motor processes produce specifiable perceptual effects.

Attempting to show that perception can be accounted for solely by visual parameters has, of course, always been very appealing to a large number of psychologists, if for no other reason than that the variables one has to deal with are relatively easy to observe and control experimentally. The neuropsychological models one considers are also simpler and more in accord with conventional stimulus-response thinking (Teuber, 1964). Postulating an interaction between motor and sensory processes in perception, on the other hand, involves additional experimental variables and more complex theoretical models. The former, simpler theories either avoid neurophysiological interpretations altogether (Gibson, 1966), or at best simply assume a retina-to-visual cortex pathway in the brain. By contrast, the latter, more complex perceptual theories posit, in addition, an active involvement of areas of the motor cortex and motor-sensory feedback systems in the perceptual process. The latter processes and connections have been less well explored.

The more complex theories of perception (henceforth called sensorimotor theories) are the ones under discussion here. Many of the relevant experiments have been reviewed extensively elsewhere (Epstein, 1967; Gibson, 1969; Gyr, 1972, 1975; Harris, 1965; Hochberg, 1971; Howard & Templeton, 1966; Rock, 1966; and Welch, 1974). The scope of this research is so vast as to preclude a detailed analysis here. Instead, some well-known prototypical studies will be briefly discussed, and the main findings and conclusions of this body of research will be summarized to provide a context for the discussion of the work by Held & Rekosh, which will be considered in some detail.

The theoretical problems inherent in assigning a critical role to motor activity in visual perception are the following. (1) It must be shown that, with visual input constant, changes in the state of the motor system do produce changes in perception. That is, motor output (efference, the efferent copy, or related mechanisms; see Bischof & Kramer, 1968; von Holst, 1954; Sperry, 1950) must be shown to be *necessary* to the perceptual process. Theoretically, there would be a potential role for the motor system in perception if the organism were to have CNS motor information at its disposal prior to the occurrence of the motor act itself, prior to the occurrence of motor-activity-induced reafferent feedback. As Teuber (1964) has suggested, if the organism has information about its own motor contribution to the construction of the stimulus, independent of action-produced peripheral feedback, one function of the response

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may be to "prepare the sensory structure for an anticipated change." (2) The second problem on which evidence must be gathered therefore concerns the issue of whether organisms are in fact able to monitor their own motor behavior at a central level [see Roland, BBS 1:1, 1978].

Experimental findings concerning whether or not motor processes are necessary in perception. The classical evidence for motor involvement in perceptual processes was provided by von Holst & Mittelstaedt (1950) and Sperry (1950). The former's studies on flies are instructive because they show that identical visual input can signal either subject movement or stimulus movement, depending on whether or not self-initiated movement by the subject is involved. If a fly is placed in the center of a black-and-white-striped cylinder rotating in one direction, the fly follows this movement by rotating ipsiversively (the optokinetic response). However, if its head is surgically rotated 180 degrees so that left and right sides of the eyes, and hence the visual signals, are reversed, the fly instead rotates contraversively. If a stimulus such as a smell is placed to the left side of a fly in a stationary cylinder, the animal will turn towards it, thereby making a movement contraversive to the movement-induced rotation of its visual array. Under this condition the fly does not exhibit the optomotor reflex; that is, the same afferent input evidently no longer signals rightward turning of the environment and hence fails to elicit ipsiversive tracking. The fly merely initiates leftward movement, stopping when it reaches the source of the smell. Von Holst and Mittelstaedt (1950) interpreted this to mean that efferent information contributes to the nervous system's interpretation of afferent input, somehow blocking the optomotor reflex. To refute this possibility, the authors repeated these experiments on the flies with their heads surgically rotated 180 degrees, reversing the visual signals; this gives rise to a contraversive optomotor reflex to cylinder rotation. When an olfactory stimulus is placed to one side of such an operated fly, it will turn toward the stimulus but then continues to rotate in that direction until exhausted. This only occurs if the environment is textured however; in a visually homogeneous environment the animal moves normally and stops at the location of the smell. These findings suggest that in the operated animal the optomotor reflex is not blocked during movement, and that the behavior observed in both normal and operated flies is a function of reafference and its relation to the activity or nonactivity of the efferent system.

Von Holst (1954) explained the results of the above experiments by postulating a built-in comparison between monitored efferent and afferent signals. According to von Holst, if the normal animal moves in one direction in a stationary environment, an efferent copy of the movement as well as the reafferent signals associated with such movement (i.e., contraversive movement of the visual field across the retina) are compared in the central nervous system. In this case these two signals, according to a convention assumed by von Holst, are of opposite sign and cancel one another. This means that this particular reafferent input will not signal changes taking place in the environment itself and will hence fail to elicit optomotor tracking. If the same afferent information is not accompanied by an efferent copy – such as when the environment moves and the fly is stationary – the meaning of the afferent input is changed and leads to ipsiversive tracking to follow the motion of the environment. If there is efference as well as reafference, but with the latter reversed as in the case of the operated flies, the two signals have the same sign, summate, and produce continuous circling.

A set of findings similar to those of von Holst was reported by Sperry (1950). Working with fish, Sperry found that strong circling tendencies were induced by surgically rotating the eye by 180 degrees. Thus, when attempting to turn left, for example, the operated fish will continue to turn indefinitely. On the other hand, a normal fish turning to the right (thereby producing the same motion-induced visual input as the operated fish turning left) shows no evidence of circling. A series of brain ablations and extirpations of the vestibular system failed to support the hypothesis that the relation between visual and motor factors was crucial. In fact, Sperry's finding that ablation of the optic tectum interfered with the optokinetic response while bilateral labyrinthectomy did not, clearly seemed to favor a purely visual explanation of the data. A labyrinthectomy – on the hypothesis of extraretinal motor factors – should have led to interference with a circling response. However, the additional outcome (consonant with the von Holst and Mittelstaedt findings) that exactly the same pattern of excitation from the retina will induce circling when the eye is rotated but not when the eye is normal, *depending entirely upon the direction of the movement accompanying the retinal input*, made a purely visual hypothesis seem unlikely to Sperry. The movement itself had to be brought in as a necessary determinant of the perceptual process. This argument, coupled with the negative findings following extirpation of the vestibular system, led Sperry to formulate the idea that the motor component arises not peripherally but centrally, as part of the efferent command eliciting overt movement. He thus proposed what might be considered to be the equivalent of von Holst's (1954) "efference copy" theory, namely, "any excitation pattern that normally results in a movement that will cause a displacement of the visual image of the retina may have a corollary discharge into the visual centers to compensate for the retinal displacement" (Sperry, 1950, p. 488).

The problem of the nature and development of the relation between motor processes and perception has also been investigated in behavioral studies on phylogenetically higher organisms. Hein & Held (1962) reared kittens with one of their eyes open only during normal, active locomotion and the other eye open only while they were passively transported over equivalent areas. Following several months of this experience, the "active" eye produced normal visually-guided behavior but the "passive" eye was functionally blind. "These experiments clearly implicate the motor system in processes regarded as sensory" (Held, 1964, pp. 308–309).

Held & Hein (1963) also found that self-produced movement is necessary for the development of visually-guided behavior. Cats prevented from executing voluntary movement during early pattern visual experience fail to show any subsequent behavioral evidence of depth discrimination on the "visual cliff" (Walk & Gibson, 1961). Kittens with early visuomotor deprivation also cannot perform visually-guided paw placement, which involves being slowly carried forward and lowered toward the edge of a table with only head and forelegs free. Only the normally reared animal displays visually-mediated anticipation of contact by extending its paw as it approaches the edge. Peripheral atrophy resulting from disuse of various organs was contraindicated by the presence of pupillary and pursuit reflexes and the rapid functional recovery once passive subjects were given their freedom. Debility specific to the motor system can also be ruled out, according to the authors, because passive subjects show normal tactile placing responses and other nonvisual motor activities.

The issue as to whether or not efferent activity is necessary for normal perception can be further illuminated by contrasting two classic experiments performed, respectively, by Riesen & Aarons (1959) and by Meyers (1964). Riesen & Aarons showed that movement-deprived kittens cannot discriminate a rotating environmental object. For their first three months these kittens were given an hour of patterned vision a day, during which they were prevented from moving head or body. They then had to discriminate a stationary target from the same target revolving, by making an instrumental locomotor response toward the correct stimulus. The discrimination task and rearing were the same in Meyers's (1964) experiment, but discrimination was ascertained not by an instrumental response but via a classically-conditioned leg flexion (elicited by shock and then conditioned to the presentation of a given visual pattern). The cats in the Riesen & Aarons study failed to discriminate the moving target, while Meyers's cats were successful. Clearly the difference was that in the former case inputs to the eye were produced by an organism in motion, with the effective solution to the task depending on the kitten's ability to discriminate inputs

produced by its own locomotor activity from inputs due to movement of the environment. Such a discrimination might (e.g., as suggested by Held, 1964) have to depend on a history of efferent-afferent comparison, of which these cats had been specifically deprived.

Much of the human research on the problem of the contribution of motor processes to perception, such as that of Held & Rekosh (1963), Festinger (e.g., Festinger, Burnham, Ono, & Bamber, 1967), and many others, had relied on studying the contribution made by *voluntary* (as opposed to *passive* experimenter-induced) movement to the perceptual readaptation of experimental subjects exposed to optically-induced visual rearrangements – e.g., by prisms systematically displacing images from their objects' true loci. Much of this work has also implicated voluntary movement as a necessary component in perceptual adaptation. We will now examine the Held & Rekosh (1963) study (H & R) in detail.

The Held & Rekosh study. The purpose of the H & R study was to reveal a link between motor and visual mechanisms in the production of visual adaptation. The starting point for their research was an earlier finding on adaptation to spatial rearrangement. Held (1961) had reported that self-produced movement of the body or the head, with associated feedback of visual stimulation, was required in order to compensate for visually-induced errors of localization. (For example, looking through prisms with base-left orientation will produce an apparent rightward displacement of objects in the visual field and leads to errors of pointing and/or gaze, which, Held reports, can be fully overcome by self-produced movements and the accompanying visual feedback.) H & R argued that prism-induced changes in shape also represent an alteration of spatial relationships in the visual field. (An example of a visual rearrangement of shape is that straight lines appear curved when first viewed through a prism. As adaptation occurs, they begin in due time to appear less curved to the experimental subject (S). Upon removal of the prism, S temporarily sees objectively-straight lines as curved in the opposite direction.) H & R accordingly reasoned that shape adaptation, like adaptation to displacement, ought to be inducible by having S experience spatial rearrangement associated with voluntary movement, but that this need not involve direct exposure to actually-rearranged curved or straight lines. It is on this point that the H & R study diverged from the rest of the literature on visual shape adaptation (e.g., Festinger, Burnham, Ono, & Bamber, 1967; Gourlay, Gyr, Walters, & Willey, 1975; Gyr & Willey, 1970; Sirigatti, 1974; Slotnick, 1969; and Victor, 1968). By not training S with actual curved contours, H & R did not need to control for other variables that have plagued the interpretation of many other studies, such as the so-called Gibson effect (Gibson, 1933), which concerns the induction of shifts in the perception of straightness after brief fixation of a curved line. The Gibson effect is thus quite independent of rearranged visuomotor feedback but needs to be taken into account in all adaptation studies in which S views curved lines.

In experiments on the perceptual recalibration of shape, S typically looks through visual or other spatial-displacement devices at contours that appear straight or curved but do not provide the perceiver with the usual visual feedback when scanned, traced with the arm, and so on. It is assumed in such studies that the initially-experienced discrepancy with habitual sensorimotor relations will adapt, leading to a change in the motor and/or visual parameters controlling the visuomotor process. For example, there has been a hypothesis that the need to make curved eye movements in order to scan and fixate an apparently straight line will modify the visual judgment of straightness.

In the H & R study S did not experience discordant sensorimotor feedback in connection with the scanning of normally straight or curved contours during training. Rather, instead of presenting a patterned field of straight or curved lines, H & R had S walk around inside a six-foot-diameter cylinder while looking through a base-left or base-right prism. The walls of the cylinder consisted of a random array of dots. This randomness was not altered by prismatic displacement. What then was altered? H & R are rather cryptic on this matter, however one could argue that S's movement would cause lateral displacement of the centroid of the retinal flow pattern. (When one moves straight ahead without prisms, the centroid of the flow falls on the fovea.) In addition, had the orientation of the prisms been up or down instead of left or right, then as S walked around inside the cylinder, the rate of displacement of the dots would not have been linear, as S would expect from normal experience. For example, under base-up/base-down conditions, distant points appearing to be at eye level would appear to move up or down (depending on prism orientation) when approached. Moreover, their apparent motion would be a nonlinear function of their distance from the viewer. This kind of information, available only from prisms oriented up or down, would seem to be germane to shape adaptation.

H & R argued, even concerning their base-right/base-left prism conditions, that the prism induces an alteration of the spatial relationships among points within the visual field. They predicted that such an alteration could then lead to changes in the perception of straightness.

H & R obtained strong and uniform results with eight Ss under active movement conditions. Not only did *all* Ss show positive adaptation (a rarity in this kind of research), but, upon release from the measuring apparatus, most of them, reported apparent curvature when fixating straight vertical contours in their normal surroundings. A control group of eight Ss under a passive movement condition showed no adaptation.

Critiques and counterstudies. Work in this general area has also elicited a number of critical comments and counterstudies. Gibson (1966), for example, has criticized the experiment of von Holst & Mittelstaedt (1950) and, implicitly, Sperry's (1950) study as well. Gibson's point is that in nature the rotation of ambient light *around* the animal, such as that experienced by von Holst & Mittelstaedt's fly, is never due to a rotation of the environment itself but is always the result of a circling motion by, or imposed upon, the animal. Thus it signals movement on the part of the animal, according to Gibson. Given this tenet, he interprets von Holst & Mittelstaedt's results as follows. In the experiment in which the cylinder moves, the animal interprets this as its own nonvoluntary motion, caused by external factors, which in nature might be wind, and so forth. It resists these external forces, and hence optokinetic movement occurs. With voluntary movement, on the other hand, the animal has the information that it is activating its own responses, which allows it to stop circling when opposite the appropriate point. With the operated fly the scenario is that it activates its own movement but then becomes aware that it is apparently also being acted on by external forces, for which it tries to compensate by optokinetic movement.

The gist of Gibson's critique of von Holst & Mittelstaedt is to deny their argument that the same afferent input (rotation of ambient light) in one case specifies movement by the environment and in the other, movement by the observer. Gibson suggests that this input always specifies motion (either voluntary or passive) by the observer. That being the interpretation, the contention that afferent information alone determines perception can stand.

With respect to the fly, there are insufficient data at this point to resolve the argument. However, at the level of human perception it can probably be said that Gibson's critique does not hold. That is, a human observer placed inside the cylinder would under some conditions indeed see the cylinder as moving and thereby have the experience that Gibson suggests the fly does not have.

Human counterstudies have attempted to show that adaptation to displacement can occur in the absence of any voluntary activity. In one study, for example, cues as to the visuomotor conflict were successfully provided in the absence of any voluntary activity by having apparently-displaced moving objects collide with the passive perceiver (Howard et al., 1965). As Taub (1968) has pointed out, however, these adaptations (in terms of a subsequent pointing response) presuppose prior well-established sensorimotor relations

and hence cannot contribute to the decision as to whether or not the efferent motor signal is necessary to adaptation.

Evidence of a central mechanism to monitor behavior. Consider next the question of whether organisms are in fact able to monitor their own motor behavior at a central level. Positive evidence on this matter would at least provide a theoretical basis for findings of motor involvement in perception. The evidence here comes from the classical studies on deafferented animals, summarized by Konorski (1967) and Taub & Berman (1968).

The deafferentation work issues from early findings reported by Mott & Sherrington (1895) and Sherrington (1931) that deafferentation of a single limb leads to its total incapacitation for any purposeful activity. These results seemed to support Sherrington's theory of the reflex arc based on investigation of the afferent and efferent spinal neuron. The work was superseded, however, by further studies with rodents, cats, and monkeys, exploring conditions under which deafferented systems do manifest purposeful activity. The newer findings forced a revision of the Mott & Sherrington interpretation.

The research was initially designed to ensure, by deafferentation of relevant parts of the spinal cord, that the animal did not get any direct proprioceptive feedback from its own voluntary movements. Subsequent research also became concerned with eliminating all indirect peripheral feedback. Examples of such indirect feedback are the sound of a buzzer signalling the onset of the animal's shock-avoidance response, skin distension with movement of the deafferented limb, and stimulation of the middle ear during voluntary activity. The concern with the elimination of indirect peripheral feedback from the animal's own activity led later investigators to expand the deafferentation so as to eliminate most of the somatic and interoceptive feedback. Moreover, there was an interest not only in gross but in fine movements as well. Finally, trace conditioning was used in an attempt to eliminate associations between voluntary movement and the conditioned stimulus.

The number of studies involved precludes a detailed review here. A summary of the major findings follows. (a) Under conditions of partial deafferentation to prevent feedback from a given instrumental limb or pair of limbs, total deafferentation plus blindfolding, or combined surgical and pharmacological interruption of the autonomic nervous system, the animals in question could be trained to produce the instrumental response; if trained previously, they retained the instrumental response or could be retrained. (b) Both gross instrumental responses such as forelimb flexion and fine instrumental behavior such as finger movement were preserved or could be trained under the above conditions. (c) Under freely-moving conditions both partially and totally deafferented animals exhibited total restoration of function. Partially deafferented animals, for example, became successful at climbing a wire mesh fence within two to six months. Totally deafferented animals showed restoration of function of the forelimb, but, because they did not survive long enough, it could not be determined whether hindlimb function would have recovered too. (d) The only restriction to be placed on the findings under item (c) above is that if only one limb was deafferented, the animal's unaffected limb had to be restrained during training. If it was not, the findings for the free-movement condition (c) did not occur. Taub & Berman's (1968) explanation for this is that the movements of the unaffected limb have an inhibitory effect on the other limb, which, due to the operation, is no longer held in check by the ipsilateral segmental afferent inflow. This problem does not arise, however, when both limbs are deafferented. (e) When a totally deafferented animal, deprived of all somatic feedback as well as all feedback from sympathetic and sacral parasympathetic pathways, was also deprived of feedback from most of the cranial parasympathetic system, it still made avoidance responses. Elimination of all feedback, however, tended to put the animal to sleep.

In summary, one can conclude from this review of theory and experiment on the sensorimotor theory of perception, that motor variables do appear important in various aspects of visual perception such as perceptual adaptation, and that research has revealed the neurophysiological mechanisms whereby the motor system might participate in perception.

The Replication of the Held & Rekosh Study

As suggested earlier, the present replication of the 1963 study by H & R was undertaken because it stood out from other studies on sensorimotor processes in visual shape adaptation, by virtue of its greater conceptual directness and elegance and the exceptionally strong findings it reported.

It would appear that such strong results speak for themselves. Nonetheless, critical evaluation of the study raises some interesting points and further problems. As mentioned above, it would appear that, for greater effectiveness, H & R should have used base-up and/or base-down prism orientations instead of the base-left and base-right they actually employed, because the latter two orientations cause the nonlinear displacements associated with curvature only under *vertical* movement of the body, while the former cause nonlinearity under horizontal movements. Since, except for some up and down head motion, walking along the cylinder wall produces primarily *horizonal* motion, the strength of the discrepant displacement stimulus would be far greater with the prism base up or down than with the lateral orientations used by H & R. Essentially the same argument has been made by Rock (1966) and by Victor (1968). Given this consideration, the positive findings obtained by H & R under the base-right/base-left conditions are even more striking. It would appear that their results can be explained only if it is assumed that in their experiment S moved his head up and down to a considerable extent while walking, or if the change of the location of the centroid of the visual flow, mentioned earlier, constitutes important information.

A second question worthy of attention concerns the conditions under which the discrepant nonlinear displacement effects would be noted by S while walking past an array of randomly distributed dots. In order to observe this particular property, S cannot merely let his gaze wander at random from one dot, or set of dots, to another while walking. Rather, he must observe discrepant displacement on the part of one *particular* dot, or the discrepant displacement and associated change in shape of a set of *specific* dots. That is, under a random distribution of dots the succession of different randomly chosen dots under transformation is also random.

Neither this issue nor the problem of base orientation of the prism was analyzed and discussed by H & R. Yet both should have considerable effect upon the outcome of the experiment.

The present replication explicitly takes account of the problem of prism orientation. Not considered in this replication has been the problem of how systematically S scans his visual field while in the cylinder. The realization that this was a relevant issue came only after the completion of the replication. As will be seen, the negative results obtained suggest the latter variable as a possibly important one.

Experimental design. The purpose of this study was, first of all, to replicate one of the experimental conditions for which H & R obtained strong positive results. The condition in which S walked around inside the cylinder, looking with the right eye through a base-right prism while the other eye was occluded, was chosen for this purpose. In addition, in order to ascertain whether, as hypothesized above, stronger results would obtain with a base-up prism, this variation was also run as an experimental condition. Pre- and post-test measures of S's straightness judgments made it possible to ascertain whether the training condition had had an effect on the perception of shape.

Apparatus. For the straightness tests the same kind of rotary prism was used as that employed by H & R. This consisted of a variable

prism whose power ranged from 20 pd base-left to 20 pd base-right. With his right eye S viewed a prismatically-displaced grating of straight black bars ⅜-in. wide and separated by white strips ⅝-in. wide. For Ss who had gone through the base-right training procedure the grating consisted of vertical bars, while Ss trained under a base-up condition were tested with horizontally-aligned bars. As in H & R, the target was viewed through a narrow-band filter (Kodak Wratten No. 61), which eliminated any prismatically-induced color fringes. Increasing the power of the prism made the bars of the grating look increasingly curved. S's task was to rotate the prisms until the bars of the grating appeared straight. The power of the prism setting for which this judgment was obtained could be read from a scale to an accuracy of 0.5 pd.

Again, in line with the H & R experiment, the cylinder within which S was placed was 6 ft. in diameter, 6 ft. high, and 2.5 ft. above the floor. S walked in a counterclockwise direction along the inside wall of the cylinder, wearing a 20-pd prism in front of his right eye. The prism was mounted on welder's goggles and provided an approximately 60-degree field of view. The cylinder was made of off-white tent canvas. On the inside of the cylinder were randomly tacked, a large number of circular red, blue, and green dots made of CONTAC paper, ¾, ½, and 3/16 in. in diameter, respectively. The maximum and minimum distances between dots were approximately 3.5 and 1 in.

Subjects. Thirty-six University of Michigan volunteer students participated in the study. Of these, half were used in the base-up and half in the base-right condition.

Procedure. S was given eight pre-tests, with the initial settings of the prism starting at −20, +20, −15, and +15 pd. This order was repeated twice so as to yield a total of eight judgments of straightness from each S. S would alter each initially-given setting until the bars of the grating viewed through the rotary prism appeared straight.

The procedure described above is in somewhat sharp contrast with that of H & R, who used only positive initial settings – that is, settings corresponding to an initial curvature in the bars of the grating that was in the same direction as that of the predicted adaptation effect. Since the use of this latter procedure did not receive any express justification by H & R, and since it fails to conform to the usual practice of counterbalancing initial test settings, the counterbalancing method was adhered to in the present study.

Upon completion of the pretests, S was led to the inside of the cylinder and the 20-pd prism was mounted on the welder's goggles over the right eye. S was asked to observe the dot patterns for 30 min. while walking counterclockwise within the cylinder with his right shoulder close to, but not touching, the wall.

Following the 30-min. exposure, S was blindfolded and led back to the test apparatus. The prism was removed from the goggles, and eight post-tests identical to the pre-test were administered.

Results. Adaptation was computed as a post-test minus pre-test shift in the pd setting of straightness. Positive adaptation as a result of base-up prism training would correspond to a tendency to shift judgments of straightness toward a curve with the center higher than the ends. In the base-right condition this would consist of a shift in straightness judgment toward lines whose midpoint had shifted to the right. A numerically positive score constitutes a score in the direction of positive adaptation in both experimental conditions.

The mean adaptation and standard deviation for the base-up active movement condition were +0.63 and 3.86, respectively. For the base-right active movement condition they were +0.34 and 4.31. Both these means represent chance effects, as indicated by t-tests, and it is clear that neither training condition produced any adaptation. The number of positive adaptors in the base-up and base-right groups was 10 and 7, respectively. This finding also goes counter to the results obtained by H & R, which showed that *all* Ss in the active condition adapted.

No adaptation was obtained by H & R for the passive movement condition. This finding rules out the possibility that the positive adaptation reported for the active movement condition might have been an artifact due to the use of unbalanced pre-and post-tests. Thus there is a rather perplexing discrepancy between this replication and the H & R study, for which an explanation must be found.

Conclusion. While the results of the replication could lead one to doubt either the findings reported by H & R or those of the replication itself, the possible cause for negative results mentioned earlier is probably worthy of exploration. That is, as was suggested, neither in the H & R study nor in the present replication was any attempt made to ensure that S systematically observed and followed the transformation of *specific* sets of points. (Admittedly, to explain the discrepancy on the basis of differences in attention poses the problem of guessing why the H & R study created more attention. No reasonable hypotheses suggest themselves.) To investigate the question of attention in some depth, it may be necessary to explore a relatively large set of stimulus conditions. Some of these should perhaps be simpler than that used by H & R (as well as this replication), which by its diffuseness and non-specificity placed an enormous attention load on S.

Two additional possibilities for further investigation should perhaps be considered. One is to replicate the replication, but with a change to ensure that the stimulus provided by the inside of the cylinder has exactly the same dot density as that in the H & R study (a parameter not reported by those investigators). Second, the results of the present replication may necessitate a further series of more refined theoretical and methodological challenges to a sensorimotor theory of perception than have been made hitherto.

In general, with the exception of J. J. Gibson, relatively few students of perception will deny that discordance between motor command and reafferent visual signals can play a role in perceptual adaptation. However, Gibson's criticism may be worthy of further attention from sensorimotor theorists. First of all, as suggested earlier in this paper, in the case of the fly and perhaps some other animals as well, Gibson's simpler model of direct visual perception may well be closer to the data than the sensorimotor model. This whole issue should be explored further. Even in the case of human experimental subjects, it is possible that a direct visual mode of perception, in which judgments are based on afferent information only, has precedence over judgments requiring the confrontation and resolution of conflict between efferent and reafferent sources of information. For example, in the case of visuomotor conflict in a pointing response, it may be that S is willing to "live with" or in some way rationalize or interpret the fact that the visual target does not look as if it is in the place where sensory information from the arm would seem to indicate it to be. If S does not actually confront and resolve the conflict, adaptation can hardly be expected. On the other hand, it is known that in certain cases a resolution of the conflict appears to be the only option that S selects. Such appears to be the case, for example, when convergence and accommodation are in conflict. S cannot perceive one object at two different distances. It may well be that the sensorimotor model, when applied to such situations, will be more readily validated. It would seem that work with the latter variety of perceptual phenomena may constitute a promising approach to the validation of a sensorimotor theory of perceptions, which, after all, still has a great deal of residual plausibility.

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***by* Bruce Bridgeman**
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Adaptation and the two-visual-systems hypothesis. I would like to offer two comments on the provocative article by Gyr et al.: the first concerns the role of motor activity in visual perception; the other discusses new data relating to the independence of sensory and motor branches of the visual system. Finally, I would like to examine possible reasons for the discrepancy in results between Gyr et al. and the similar H&R study.

In the context of Gyr et al.'s discussion there is no question that motor activity plays a role in perception. I will add one additional bit of evidence to that given by Gyr et al., by reinterpreting one of the most common observations used to differentiate the perceptual effects of active and passive movements in perception. This is the simple demonstration that pushing on the eyeball with a finger results in an apparent motion of the visual world. Normally this is interpreted as a motion of the retinal image without a concomitant eye movement, resulting in an apparent motion of the world in the context of efference-copy theories. I submit that the circumstances of the demonstration can be the exact reverse of the traditional interpretation. To show this, find a fixation point and push slowly on the eye: most people have no difficulty in maintaining fixation despite the apparent motion of the world. But the actual motion of the image on the retina is then minimal, limited to the few minutes of arc of "retinal slip," and a substantial movement of the world is perceived without a substantial movement of the retinal image. The interpretation of the motion effect must now be reversed, for the only effect on the visual system is not sensory but motor: as one pushes harder and harder on the eye, the extra-ocular muscles must work harder and harder to maintain fixation, and it is the muscle action, not the image movement, that results in perceived motion of the visual world. Whether it originates from an inflow or an outflow signal, only the extraretinal signal changes in a way that corresponds to the perceived motion.

The situation is not as unnatural as it seems at first, for the foveal stimulation becomes similar to that found in pursuit tracking, where a small retinal slip acts as an error signal to initiate and maintain pursuit eye movements (I thank Ian Howard for pointing out this similarity). The crucial difference for the problem of motorsensory feedback is that no relative-motion cue is available to the perceptual system, as would normally be the case during pursuit (Gibson 1966 *op cit.*), but apparent motion is still obtained. Thus the motor cue alone, without relative motion, can induce a perceived motion very like that experienced in more naturalistic motion stimulation.

My second comment expands on Gyr et al's point that in cases of sensory motor conflict the subject (S) may be willing to "live with" the discrepancy under conditions that do not induce adaptation. Recent evidence from my laboratory confirms the idea that sensory and motor-oriented aspects of visual function can be influenced independently under the proper conditions. We began with the phenomenon of saccadic suppression of displacement (Bridgeman, Hendry, & Stark 1975), which showed that Ss sometimes fail to respond to target displacements of up to 4° if the displacements occur during large saccadic eye movements. This implied that information about the positions of objects in visual space was degraded by saccades. Yet we know that humans are not disoriented after saccades and can function quite adequately in space while making large numbers of saccades. We combined these two discrepant observations into a single experiment with the hypothesis that information about position could enter the motor-visual system without influencing the cognitive system (Bridgeman & Lewis 1976). A subject would press a button whenever a continuously-visible target was flipped 2° to the left or right; sometimes S would fail to press the button because of the effect of a saccadic eye movement. Following either a detection or a failure to detect the displacement, the experimenter could extinguish the target, thus providing S with a signal to point to the position of the

target when it had disappeared. S pointed with an unseen hand into a blank field, forcing him to use only the internal calibration of the motor system for pointing. The somewhat surprising result was that Ss pointed accurately whether or not they had detected the target displacement in the button-press phase of the experiment, showing that the motor system could receive information that was masked from the cognitive system. A second experiment used a criterion-free measure to show that Ss could not detect the target displacement under these stimulus conditions.

The implications of these results for the Gyr et al. paper are clear: Held himself, a few years after the publication of the H & R study, gave some of his deprivation experiments in kittens a similar interpretation in terms of two visual systems (Held 1968). We have demonstrated a similar independence of function in the normal human—the realm of the Gyr et al. and the H & R studies.

The problem remains why H & R obtained adaptation in their active condition while Gyr et al. did not. A close reading of the two experiments yields only one significant difference in method not mentioned by Gyr et al.: the latter used small circular dots to construct their texture, while H & R used "small spots of irregular shape." It is possible that the irregular shapes underwent perspective transformations that were more salient to Ss than the rather subtle transformations of a circular patch. Unfortunately, neither of the experiments specifies the angular size of the spots at S's eye, but in the Gyr et al. study, where the largest dots were ¾" in diameter, I conservatively estimate the angular size to be 1½° (assuming that the observer is facing perpendicular to a radius of the drum, halfway between its center and its edge). If the spots were of similar size in the H & R study, foveal resolution would easily be adequate to resolve perspective transformations in individual dots, even if Ss were unaware of this cue. Thus any replications of this important study should use true point-sources of light as texture elements, perhaps by backlighting pinholes in the drum. This would be the most powerful test of the H & R hypothesis.

by **Clarke A. Burnham**

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Adaptation to curvature in the absence of contour. The H & R study on adaptation to the curvature produced by prism spectacles is important because, as Gyr et al. note, Ss did not view contours. Gyr et al. have performed a valuable service by attempting to replicate this study. Unfortunately, the results of their replication do not permit one to specify the experimental conditions that will produce adaptation, although the authors hypothesize that "attention" may be a relevant variable.

What conditions lead to adaptation and what conditions fail to do so? Previous adaptation studies, reported by Festinger et al. (1967 *op. cit.*) and by Gyr and his associates, have found that adaptation occurs when Ss actively attend to the contour in performing their experimenter-imposed tasks. In those studies, Ss who failed to adapt were making analogous active movements, but they were doing so independent of efferent commands coded with respect to the contour. In neither the H & R study nor the Gyr et al. replication did Ss need to attend to the differential displacement (curvature) and make movements with respect to it. Ss in the H & R study may have done so, but they apparently did not have to. Perhaps adaptation occurs only when Ss learn new afferent-efferent associations.

This conjecture would be more reasonable if there were clear evidence that, even in the absence of contours, people adapt to the curvature produced by prism spectacles when required to perform a task designed to promote the learning of new afferent-efferent associations. I have conducted a study, currently unpublished, which found adaptation in the absence of contours. This commentary is a brief description of that study.[1]

S's task was to shoot a "machine gun," emitting a collimated burst of light when a trigger was depressed, at targets (small dots) flashed on a screen. During the task Ss wore prism spectacles with the base mounted upwards. They were unable to see any horizontal or vertical contours. Two independent variables were investigated in a 2 × 2 factorial design.

The first independent variable involved the manner in which the targets were presented. Consider S's behavior in one of the target presentation conditions (which will be descriptively termed the "single-flash" condition). He has just shot at a target near the right side of the screen. A new target is presented to his left. As S swings the gun to aim at this target, it will rise in the field of view, due to the prism-induced curvature. As long as this new target remains visible while S swings the gun to the new location, he can monitor the discrepancy between the current vertical position of the gun and the new target position. S can thus use this information to adjust the position of the gun as he moves it across the field.

Under the above conditions S will not have to relearn relationships between the visual locus of a target and the efferent activity necessary to effect a movement to that locus. However, there is a slight modification of the task that would be expected to necessitate learning new afferent-efferent associations: as before, a new target is presented after S shoots at the first. But as soon as S begins to move to the new location, this target disappears, to reappear only when S has reached his apparent location. On initial trials, S would be aiming below the position at which the target reappears and would have to make a corrective upward movement. After some experience with this situation, S would presumably be able to move directly to the position at which the target reappears; he would have learned new afferent-efferent associations. This target presentation condition may be descriptively termed the "double-flash" condition. (The experimenter controlled the aperture of the slide projector, presenting the targets so as to make them disappear and reappear.)

The other independent variable involved the efferent command issued to the extra-ocular muscles. When S is wearing prism spectacles, this efferent information is inconsistent with that issued to the head, torso, arms, and so forth. If, when S is wearing base-up prisms and viewing an objectively-straight, horizontal contour, he is asked to scan along it without making any head movements, his eyes will move in a curved path. The eye movements are consistent with the distorted array, and hence would not, by themselves, produce adaptation. If S is somehow forced to scan the array by moving his head from side to side and keeping his eyes stationary, his head will move in a straight path. If he is allowed to move both head and eyes, efferent output to the muscles would be a mixture of commands to move the head in a straight path and to move the eyes in a curved path. Since efference to the extra-ocular muscles might well be more intimately involved in determining perception than efference to the neck muscles, free scanning might result in less adaptation than would occur in a condition in which eye movements were minimized. In the machine gun study eye movements were minimized for one-half of the Ss by the use of an artificial pupil (a small hole in a sleep mask worn behind the prisms). In this condition Ss were able to see the entire field when gazing straight ahead. If they moved their eyes to foveally fixate a peripherally-glimpsed target, however, the target would no longer be visible. The light rays from the target would no longer pass through the artificial pupil and the pupil of the eye. Hence the artificial pupil would be expected to produce a reduction in saccadic eye movements. No such restriction was imposed on the other Ss.

A few more details: There were ten male Ss in each of the four conditions. They viewed the targets monocularly while wearing 30° prisms mounted base upwards in welder's goggles. The possible target positions subtended a horizontal visual angle of 21° and a vertical visual angle of 9°. There were two six-minute shooting periods, separated by a three-minute break during which S rested with his eyes shut. S shot at approximately 200 targets. Adaptation was measured by changes in the pre- to post-test settings to apparent straightness of a grating of horizontal lines viewed through an adjustable (Risley) prism. It is extremely unlikely that this measure, a measure of the after-effect of adaptation, would reflect conscious error correction.

The results were clearcut. Only those Ss whose eye movements were restricted and who were in the "double-flash" condition adapted to the curvature. Their mean adaptation was 4.25 pd, with a standard deviation of 4.27. This amount of adaptation is significantly different from zero and is also significantly different from the amount of adaptation in the other three conditions, which amounted to −0.20 pd in the free eye movement/single-flash condition, 0.77 pd in the free eye movement/double-flash condition, and 0.85 pd in the restricted eye movement/single-flash condition. Of course, additional exposure might have resulted in significant adaptation in these latter two conditions.

These data show that under some conditions adaptation to the curvature produced by prism spectacles does occur, even in the absence of contour. Two variables have been shown to affect the magnitude of this adaptation. Adaptation occurs when eye movements are restricted and when S is required to learn a new set of commands to the musculature controlling the head, torso, and arms in response to the altered visual input.[2] Why did H & R obtain adaptation while Gyr et al. failed to replicate their finding? I would hypothesize that the stimulus environments and instructions used in the studies were sufficiently different so that the participants viewed and processed the dots in different ways. It should be noted that S's movements in the Gyr et al. study were constrained; they walked around the drum in a circular path and remained near its perimeter. Ss in the H & R study were apparently able to move more freely within the drum (Held 1965). These are speculations, however. What we need is more experimentation to delineate the conditions that facilitate adaptation.

NOTES

1. A detailed report of the study is available from the author.

2. An earlier manuscript of this study failed to be accepted for publication because a referee very correctly noted that the greater adaptation with restricted eye movements may have occurred because the manipulation to reduce eye movements could have increased head movements. However, I have since conducted a control study in which I measured S's head movements in the restricted and unrestricted eye-movement conditions. The head movements did not differ.

The necessity to swing the head and torso behind the sights of the machine gun was probably responsible for the equivalence of the head movements. The difference in adaptation between the free and restricted eye movement conditions may be attributed to the presence versus absence of saccadic eye movements. When a new target was presented, the Ss in the free eye movement condition would initiate the body and head movements necessary to swing the gun toward the target and, simultaneously, initiate a saccade to foveally fixate it. The efference issued for these two sets of movements would be inconsistent, and the efference issued to the extra-ocular muscles would be consistent with the distorted array. If the efference to the extra-ocular muscles is more intimately involved in determining perception, the presence of efferent commands to the extra-ocular muscles consistent with the distortion would minimize adaptation. Ss in the restricted eye movement conditions learned that they should not make this saccade, since it caused the target to disappear from view. Adaptation would be produced by the altered efference to the body and head.

***by* Brian Craske**

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A stationary subject* does *perceive curvature when wearing a prism in a spotted drum. The background to the reported studies consists of early work on adaptation to laterally-displacing prisms that suggested a link between adaptation of perceived direction and prior active movement. The necessity for such a link has long since been denied (Craske 1967; Pick & Hay 1965; Singer & Day 1966b; Templeton et al. 1966; Weinstein et al. 1964). Changes in registered eye-in-head position, which underlie part of this kind of adaptation, are not logically related to pattern perception, which is the class of phenomena to which the perception of straightness (with eyes stationary) belongs. Thus even if motor activity were a necessary condition for changes in registered eye-in-head position, its necessity for perceiving straightness is wholly speculative.

An examination of the rationale for the experimental protocols in the original H & R study reveals considerable confusion. The argument is essentially as follows. When S wears the base right or left (BR or BL) prism, it curves verticals in the outside world, but in the drum the random dots undergo an identity transform and there are no perceived curves or changes, except when S moves. During movement there is a complex transformation of the visual input, which with active movement can lead to adaptation and an after-effect of bowing of verticals. This argument is both mistaken and misleading, which should be made clear by what follows.

In order to consider the effects of wearing BR prisms in the drum, I constructed a facsimile with a spot density of 2/cm^2. The most pertinent observation is that, with a 20-dioptre BR prism over the right eye and a 60° field of vision, S's impression of the cylinder is that it *looks like the inside of a barrel;* the surface defined by the spots is curved away from S. This is so whether or not S is moving around the cylinder. This directly contradicts the idea that there is an identity transformation when inspecting random dots via a prism. When moving around the perimeter (which is easily accomplished and does not require seeing one's body), the path of S's gaze takes the form of a chord of the circle. When I acted as S, I used frequent saccades of 25 to 35 cm. The visual array was noticeably compressed on the right-hand edge, thus the flow of images over the retina was not uniform in speed but was *orthogonal to the stripes used to test for adaptation* in the reported experiments. Two points emerge from this: 1) Merely standing in the cylinder puts S into a curved environment: this is likely to generate Gibsonian after-effects whether or not S remains stationary. 2) Movement seems unlikely to produce retinal stimulation that is at all relevant to subsequent perceived change in the straightness of verticals.

An unanswered question is why any investigator would expect changes in straightness of verticals *in particular* as a result of the visual input resulting from movement when wearing BR prisms in the drum. I do not know the characteristics of the visual input in this case, and I have not seen an analysis of such a complex situation: if these things are not known, I fail to understand *how* a prediction about an after-effect in the perceived straightness of verticals could have been made on the basis of the obvious characteristics of the retinal-flow pattern, irrespective of whether this was contingent upon movement. Indeed, it is a most unusual experiment that predicts that the unknown characteristics of a stimulus will have any specific effects. Gyr et al. are also perturbed about this problem: "It would appear that the H & R results can be explained only if it is assumed that . . . S moved his head up and down to a considerable extent;" such movements, however, are not typical of human locomotion.

As a result of this disquiet, Gyr et al. introduced a base-up (BU) prism and a horizontal test for perceived curvature. This is appropriate because in the experimental condition the trajectory of a given spot will move up as it gets closer to S, thus providing an opportunity for the occurrence of horizontal curvature adaptation. My own experience in the cylinder while wearing BU prisms, however, brings to light a further problem. Under these circumstances the shape of the visual world consists of a flared flowerpot, the effect being particularly pronounced when one is standing near the perimeter apparently looking along a chord. This perceived shape is again likely to produce regular curvature adaptation, *for verticals or near verticals* (not horizontals), whether or not S is moving. For both BR and BU exposure I would predict strong Gibsonian adaptation for grating-test stimuli of length and distance appropriate to those seen in the experimental situation.

There is one other question, namely: whether the spatial distortion of the cylinder can always be perceived by S. This could possibly be a function of spot density; it is likely that the lower the density, the less visible the apparent shape of the surface. This may account for Gyr et al.'s failure to find significant (Gibsonian) adaptation in the BR condition. After the BU condition, however, there was no appropriate test for this form of adaptation. The failure to obtain adaptation in the BU test suggests that even given this appropriate experimental situation for the production of movement-contingent curvature adaptation, the speculation as to its occurrence was incorrect, as indicated in the opening paragraph.

H & R's positive results for the active case probably amount to normal curvature adaptation; I cannot see how the stimulus conditions could allow for anything else. The failure to obtain adaptation in the passive condition is more mysterious but could well reflect the lack of attention or motivation that Efstathiou (1963) first noted could be absent in the passive condition.

In conclusion, it would seem that no clear case has been made for the role of movement (other than eye movement) in the perception of form, and I am not surprised that these replications failed to find any. The H & R methodology has been used without analysis of the characteristics of the visual input to the system, and for BR and BL prisms it is not clear that any component of such input will yield the kind of information necessary for the brain to adapt the part of its perceptual system that is concerned with the straightness of verticals. Finally, the experimental situation is neither elegant nor powerful. The drum is far from providing "an environment specially patterned to prevent the appearance of curvature when viewed through a prism" (Held 1965). There is ample curvature information with a 2/cm^2 spot density; thus conventional curvature adaptation is likely to be present.

***by* R. H. Day**

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What is self-induced motor activity adapting to? Gyr et al. are quite right to regard the H & R experiment on visual adaptation to prism-induced curvature as important from the standpoint of the sensorimotor theory of space perception. This experiment, together with two on prism-induced tilt by Mikaelian & Held (1964) – apparently submitted earlier but published later – were interpreted as overcoming a major difficulty for the theory, or rather for the valid testing of the theory. Gibson (1933 *op. cit.*) and Gibson & Radner (1937) had shown that during prolonged inspection of curved (or tilted) lines, perceived curvature (and tilt) diminishes (adaptation), and that after inspection, straight vertical lines appear curved (or tilted) in the opposite direction (negative after-effect). Gibson showed that these effects occurred either when the lines were actually curved (or tilted) or when straight lines were rendered so by prismatic refraction. Thus, in proposing a second and independent class of adaptation involving self-induced movement while viewing through wedge prisms (Held 1961 *op. cit.*, 1962), it was necessary to show that such adaptation occurred under conditions that could not give rise to sensory adaptation and after-effect, as described by Gibson.

Mikaelian & Held (1964) claimed to have achieved this for object orientation by requiring subjects (Ss) to set a bar to apparent verticality before and after active and passive exposure to randomly arranged, dim, luminous spheres hanging in a darkened room. A small (2.1°) but significant shift in the apparent vertical

occurred after Ss walked about the room, but not after they were moved about while standing on a trolley. Following a challenge by Hochberg (1963), Held & Rekosh (1963 *op. cit.*) made a similar claim for sensorimotor adaptation to curvature, as described by Gyr et al. The latter have failed to confirm the earlier finding. Incidentally, this is bound to call into question the results from Mikaelian & Held's experiment on apparent verticality.

Two issues arise from Gyr et al.'s experiment: possible reasons for the inconsistency between the original experiment and its replication, and the logic of the argument on which the original experiment rests.

On the first issue it can be argued, of course, that failure to confirm the original outcome is attributable to lack of exactness in repeating the earlier conditions. However, this implies also that the original positive outcomes derived, not from self-induced locomotion during a period with prismatically-distorted input (which was faithfully reproduced in the replication), but to some unidentified variable. Thus, to argue that the conditions were not *exactly* the same is to imply that the original results are not robust and lack generality. Another possibility that must be raised concerns the expectations of both Ss and experimenters. There is now an impressive body of data (Rosenthal & Rosnow 1969; Rosnow & Rosenthal 1970) to show that what Ss and Es expect to occur can markedly bias the outcomes of an experiment [see Rosenthal & Rubin: "Interpersonal Expectancy Effects" *BBS* 1(3) 1978]. Further work would be needed to establish the basis of the inconsistent findings.

The second issue is more fundamental and relates to the sensorimotor theory itself. To prevent the occurrence of purely sensory adaptation and aftereffect as described by Gibson (1933 *op. cit.*), Mikaelian & Held (1964) and H & R used stimulus arrays consisting, respectively, of randomly-arranged, hanging spheres and randomly arranged and randomly-shaped wall elements. As Gyr et al. point out, H & R are cryptic on the question of what particular aspect of the stimulation was thereby altered by prismatic refraction. Gyr et al. suggest that it might have been the centroid – that is, the focus of expansion – of the retinal flow pattern. However, Johnson, White, & Cumming (1973) have shown that this focus is very difficult to judge, and errors are usually quite gross. Thus the question that has to be asked is: If changes in curvature and orientation due to refraction are not discriminable in random patterns, what then is rearranged? It seems odd to expect adaptation to rearrangement to occur if no rearrangement is discernible.

There is a paradox here. On the one hand it has been argued repeatedly and forcefully (although the argument is now in question) that for sensorimotor adaptation to occur, motor activity must be self-induced – that is, it must be commanded and deliberately-initiated activity of which the observer is presumably aware [cf. Roland: "Sensory Feedback to the Cerebral Cortex During Voluntary Movement in Man" *BBS* 1(1) 1978]. However, it appears that on the sensory input side the change to which adaptation occurs can be almost or wholly unnoticeable. That is, the observer presumably need not be aware of any alteration. Therefore, the question: What is self-induced motor activity adapting *to?* is fair and relevant. The data reported by Gyr et al. indicate that adaptation does not occur at all under such conditions. This hardly seems surprising, since there is no discriminable change in stimulation to which the motor system can adapt.

One final point is worth making. Pick & Hay (1964) pointed out that wedge prisms give rise to a number of distortions, including displacement of the image, curvature, spectral dispersion, differential image displacement with angle of regard, and tilting with head movement. They found that after three days of continuous wearing, adaptation to curvature was only 11.2 percent, while that to horizontal displacement was 44.6 percent. It is conceivable that after a mere 30 minutes of exposure to curvature, the adaptation, if any *did* indeed occur, might not have developed sufficiently to be reliably measurable. A similar experiment involving a random array, but measuring the much greater adaptation to displacement, might therefore be worth performing.

by **Sheldon M. Ebenholtz**

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Insufficiencies in perceptual adaptation theory.

1. The problem of replication failure:

a. The direction of the subject's movement in the replication was such as to place the viewing eye adjacent to the patterned surface. The direction of movement is not reported in the original study. Such a potential procedural difference may have an indirect effect on attention and fixation patterns.

b. Held & Rekosh (1963 *op. cit.*) reported that, ". . . movements of the head alone, if of sufficient amplitude and deviation, sufficed to produce an adaptive change . . ." (p. 722). Although H & R instructed subjects ". . . to minimize movements of their heads in relation to their bodies . . ." (p. 723), it remains plausible that the occurrence of compensatory eye-head movements may hold the key to replication. If so, the importance of fixation on a specific target during locomotion would be critical, not merely for the purpose of *noting* the target movement path (as Gyr et al. suggest), but for the purpose of retraining the eye-head movement system.

c. A carefully-planned replication that fails, such as that of Gyr et al., indicates that the phenomenon at issue is not as robust as it was believed to be. This means that the relevant variables and boundary conditions have not yet been sufficiently isolated – but it also implies that theory as thus far developed has been insufficient for the facts. Another issue making the same point is the failure to obtain 100% adaptation after lengthy exposure to optical tilt. Full compensation was first reported by Mikaelian & Held (1964). There are now almost two dozen published studies of tilt adaptation, yet none serves to corroborate the existence of complete tilt adaptation. Furthermore, my own observations on hundreds of subjects, including fast and slow adapters, naive and experienced subjects, and a variety of experimental conditions, have failed to yield a single instance of full compensation. Rather, asymptotic performance well below 100% seems to be the rule. We require a theory of adaptation to explain these facts, as well as the conditions under which full compensation is to be expected. The lesson to be drawn is that the phenomena of our science deserve more attention than they are now receiving; our theories should be less "ideal" and more empirically based.

2. Inadequacies of afferent-context theories of perception: In addition to the studies of von Holst and Sperry described by Gyr et al. (and Gyr 1972 *op. cit.*), which entail movement-correlated optical input, there are several classes of research studies that rather compellingly implicate *static* posture in visual perception. Consider, for example, the following, chosen from among the perceptual constancies: a. the constancies of object orientation (Ebenholtz 1977); b. the widely known effects of convergence on perceived size and depth; and c. visual position and visual direction constancy (Shebilske 1977).

All of these phenomena require the registration of ocular direction. It is particularly clear that when bright targets in a reduced field are viewed, only proprioception can provide the basis for apparent stability, visual direction, and orientation. The obvious conclusion is that there do exist classes of visual phenomena, some of which are determined largely by the afferent visual context; but there are other classes that require the processing of afferent context by events on which they are conditional, the latter frequently being proprioceptive in nature. Thus, afferent context theories are inadequate if applied to the entire space-perception domain.

3. The need for empirically-based theories of perceptual adaptation: A second type of eclecticism recommends itself in the distinction between sensorimotor theories of *perception* and sensorimotor theories of *adaptation.* It is clear, as in the case of afference-based theories, that not all perceptual phenomena can be appropriately treated by sensorimotor theory. Thus color vision, brightness perception, sensory after-effects associated with specific feature detectors (such as thermal adaptations, disparity after-effects, tilt after-effects, motion after-effects, and McCullough-type after-effects, etc.) may all be treated by afference-based theories, with sensorimotor theory for the most part irrelevant to these phenomena. Likewise, even within the limited domain of perceptual adaptation there is little reason to consider that all the phenomena of perceptual adaptation will be relevant to a single type of theory. Consider, for example, the direct evidence (Redding 1973a; 1975) that displacement adaptation and adaptation to optical tilt are quite independent phenomena, in that their simultaneous occurrence produces no interaction whatsoever. Furthermore, the same subjects fail to yield significant correlations across the two tasks, whereas each task indeed correlates highly and significantly with itself over time (Redding 1973b). Such differences warrant skepticism as to whether any extant theory – sensorimotor or afference-based – will be relevant to both phenomena.

Skepticism should be extended further to the very question of the identification of the locus of adaptation-like phenomena. On this point the finding of hysteresis effects associated with the tonus-control mechanisms of the extra-ocular muscles (Ebenholtz 1974; 1978; Ebenholtz & Wolfson 1975; Paap & Ebenholtz 1976; 1977) raises the possibility that the after-effects associated with eye-specific adaptation, displacement adaptation, adaptation to altered convergence, and still others, are phenomena that represent neither a remapping in the sensorimotor domain, a pure visual shift (i.e. a projection-level phenomena), nor a rescaling of the metric underlying proprioception.

The culmination of the application of skepticism as herein advocated should be the development of empirically-based theories of perceptual adaptation that encompass the major facts and functional relations generated by the study of

perceptual adaptation phenomena. The same prescription applies no less to theories of space perception in general.

by **Ronald A. Finke**

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Nonrandom curvature adaptation to random visual displays. I wish to suggest a few proposals as to how the apparent contradiction between the H & R study and Gyr et al.'s attempted replication might be resolved experimentally. First, if one maintains that the results of an earlier study are due to some uncontrolled artifact, then one should attempt to employ experimental procedures specifically designed to maximize whatever effects that artifact is supposed to produce. In particular, Gyr et al. speculate that head movements ought to be a crucial factor in determining the amount of curvature adaptation. Perhaps they should repeat their experiments with subjects intentially moving their heads horizontally or vertically during adaptation procedures. Gyr et al. also speculate that attention to the transformation of specific dots or dot patterns during movement should be a crucial factor in producing curvature adaptation. Perhaps they might consider repeating their experiments so as to maximize attention. Another factor to consider is how rapidly subjects walk around the circular display field. Certainly the rate at which dot patterns pass in front of the observer should affect the perceptual salience of nonlinear distortions produced by the prisms. If one found that, when their alleged effect upon curvature adaptation is maximized, any of these factors actually produced significant increases in the amount of adaptation, a strong empirical case could be made that differences in the outcomes of the two studies were due to differences in how that particular variable had been controlled. Otherwise, the null results of an attempted replication reveal nothing.

Second, if the problem of replication does not lie in differences between adaptation procedures, perhaps it lies in differences between testing procedures. For example, the particular width of the bars used in the test gratings might be important, given the possibility of a spatial-frequency-dependent effect. Perhaps by using different sizes and separation distances of the dots in the display field, crossed with different test-grating spatial frequencies, one could demonstrate that the obtained discrepancy is attributable to uncontrolled differences in spatial frequency matching.

Finally, I would think that at least one important prerequisite for attempting a replication is a demonstration that one's procedures work for a standard effect. Perhaps Gyr et al. should repeat their experiments using actual contours in the display field, in addition to random dots. If no evidence is found for adaptation even with actual contours, then an obvious procedural flaw has been overlooked. Indeed, before making too much of a failure to replicate, the sensitivity of one's procedures should first be substantiated.

by **David Freides**

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Motor factors in perception: Limitations in empirical and hierarchical analysis. Gyr et al. treat the H & R study as an *experimentum crucis* and conclude that they cannot replicate its results. They appear unable to decide whether to retreat massively or just a little from the theoretical position they have heretofore held. My reaction, in general, is to get away from the high drama of their presentation. I will discuss some empirical issues and then a matter of theoretical orientation.

Gyr et al. describe the earlier experiment as a between-subjects design, the passive control condition occurring in an independent group. Actually, the same eight Ss served in both active and passive conditions, and with prisms in both base right and left orientations. The only independent control group consisted of three Ss who were run in an active condition without prisms. Thus the experience of H & R's experimental Ss was quite different from that in the replication in which each S experienced only one condition; and overall, only one of the previous experimental conditions (right, active) was repeated. Nevertheless, it appears that the earlier findings were indeed replicated in seven of 18 Ss in the base-right condition, and that ten of 18 Ss adapted with base-up prisms. Failure to replicate in all Ss implicates uncontrolled interactive individual differences (note that variance is high relative to means) or inadequate procedural controls or both.

Gyr et al. discuss a number of possible procedural factors that might account for the discrepent results. I would add inadequate control of the locus of gaze, which was not objectively constrained (collars?) in either experiment. I find it difficult to imagine that some Ss walking alone in a circle for half an hour would not attempt to look at their limbs or torso despite injunctions to the contrary.

Viewing unreplicated experiments with unstudied parameters as crucial disregards the recurrent experience of replication failure. The place in the scheme of things of a particular experimental finding is secure only if it recurs as its parameters are studied in detail. In this instance Gyr et al. refer to no data about stimulus parameters (e.g. duration of induction, eye stimulated, degree of prism distortion, instructions and explanations about the experiment), response parameters (e.g. type of response used to index perception, persistence of induced effect and interaction with measurement operations), or subject variables (e.g. sex, handedness, eye dominance, age, intelligence, field independence). Such information might permit a more definitive judgment as to the heuristic significance of the original experiment. It might also provide clues to, or even explain the mechanisms that mediate the after-effect.

Gyr et al. seek evidence for the modification of perceptual or input mechanisms by recent motor-sensory experience. An alternative hypothesis might be that behavior after motor-sensory input derives from altered response mechanisms, particularly receptor-orienting behavior. For example, it is possible that some type of nystagmus or change in eye or lens muscle tone is induced by prisms, and that this varies with whether or not Ss have to look where they are going. Parametric studies would bear on this hypothesis. Cegalis (1973) found accommodative changes after five minutes of walking with base-left prisms and has related prism distortion to field dependence (Cegalis & Young 1974).

From a purely theoretical perspective, there is a disquieting feature in Gyr et al.'s presentation. As the empirical data base for the concepts of efference and reafference, they cite work done on the fly and the fish. What they do not communicate is that even if humans share characteristics with flies, they are, in other respects, likely to be quite different. That is, humans have sophisticated, flexibly-deployable neural mechanisms, deriving from later stages of evolution, which function in parallel, inhibit and supersede, or are integrated with any existing primitive mechanisms. This rather obvious idea requires theoretical consideration of some kind of hierarchical organization in information processing and motor mechanisms (*cf.* Easton 1972; Evarts 1973; Watson 1978). The gap is surprising, since in an earlier paper (Gyr 1975, *op. cit.*) discussion of "epistomological considerations" would appear to imply such an approach.

If, in a hierarchically-organized, sophisticated organism, behavioral evidence is sought for the operating characteristics of its primitive mechanisms, a formidable experimental challenge may be present. In order to study the primitive mechanisms, the means have to be found to circumvent those most effective adaptive resources that are likely to dominate the repertoire. A reliable analysis of primitive mechanisms by means of voluntary behavior may be impossible for this reason, and it may be necessary to resort to other means of observation. One precedent may be the study of human habituation – an information-processing mechanism shared with invertebrates. Measurement here is by means of psychophysiological methods of autonomically-mediated reactions in Ss who have been given no deliberate task to perform (*cf.* Gruzelier & Venables 1973). With regard to the hypothesis suggested above, a definitive test might be possible only with electromyographic recording of changes in eye-muscle potentials or some physiologic measure of accommodative mechanisms.

We remain indebted to Gyr for keeping the issue of the role of motor factors in perception alive. It shows up, I believe, as an unresolved question in such disparate areas of psychological inquiry as field dependence (Witkin & Goodenough 1977), which must have something to do with biases in the resolution of discrepent visual and somatosensory information; learning disabilities (Ayres 1972), where motor dysfunction is often observed but has a puzzling relationship to information-processing dysfunction; schizophrenia, where somatosensory, vestibular, and thought impairments often covary (Prescott 1971); signal-detection theory, where it appears that acuity may, after all, not be totally independent of response bias (Clark 1976); and in the very general and recurrent finding in sensory and perceptual research (including research on hemispheric specialization) that the response used to provide an index of information processing significantly affects and often determines the results (Freides 1974; 1977; White 1972).

by **Ralph Norman Haber**

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When is sensory-motor information necessary, when only useful, and when superfluous? Sensory-motor theories of perception drew their original impetus from the need to explain various constancies of visual perception in the face of changes produced by observer motion or orientation. Visual-orientation constancy, our ability to perceive visually the gravitational upright, has been assumed

to depend upon corrections based upon gravitational detectors in the vestibular system (Ebenholtz 1977). Visual-direction constancy, our ability to perceive the visually straight ahead, has been assumed to depend upon corrections based upon eye position in the head (Matin 1976b). Saccadic suppression, the momentary loss of visual sensitivity beginning just prior to the onset of the saccadic eye movement, has been assumed to depend upon neural signals from the eye-movement control centers initiating the saccade (Riggs 1976). Motion constancy, in which the displacement of the retinal image across the retinal surface is not perceived if caused by pursuit or saccadic eye movements, has been assumed to depend upon efferent signals from the eye-movement control centers, cancelling the effects of visual afferent displacements (Festinger et al. 1967 *op. cit.*; von Holst 1954 *op. cit.*). Fixation maintenance, our ability to maintain fixation on an object in space even when our head and body is moving in space, has been assumed to depend upon an interaction of afferent visual and efferent oculomotor control signals. Fixation maintenance is a component of the more complex sensory-motor coordination required under rapid locomotion, such as trying to catch a fly ball on the run (Melvill-Jones 1976). Finally, sensory-motor interactions have been assumed to be critical components of adaptation of visually-rearranged environments. While the natural environment does not normally undergo visual rearrangement (except for adaptation to frames of spectacles, to optically-correcting or tinted lenses, to vision under water while wearing a diving mask, or to suddenly-induced optical errors of accomodation or astigmatism), rearrangement tasks have been a favorite laboratory procedure to test for the presence of sensory-motor interactions. The recent reviews by Welch (1974 *op. cit.*), Lackner (1977), and especially Welch (1978) provide evidence that self-initiated motor activity (that producing efferent signals) may not always be necessary, although the vast majority of evidence suggests that active movement is more useful than passive movement to produce perceptual adaptation.

Gyr et al. contrast a sensory-motor theory of perception with one making no demands on a necessary motor contribution. The only reference they cite is Gibson (1966 *op. cit.*), who has the most developed visual theory of visual perception. Gyr et al. describe two theoretical conditions that would demonstrate the necessary involvement of motor activity: evidence that with constant visual input, changes in motor activity produce changes in perception; and evidence that perceivers can monitor their motor activity in order to integrate that information with visual information.

I do not feel that these conditions are a sufficient basis for claiming that sensory-motor interactions are necessary. Furthermore, Gyr et al., along with most other researchers, have failed to appreciate one of Gibson's theoretical demands on all theories of perception. Virtually all research on the motion constancies, on sensory-motor correlations, and on adaptation to rearranged visual stimulation, has tested perception in highly-restricted and artificial visual environments. Under such conditions the visual system is deprived of many of the sources of information upon which it typically and regularly relies. When this occurs, either in the laboratory or naturally (as when one is trying to see in the dark), there are two possible resulting effects on perception. If perceptual processing is based upon rigidly-ordered structural steps, then perception fails, with gross errors of perception occurring in such impoverished environments. On the other hand, if perceptual processing is based upon some flexible set of strategies, then when some sources of useful information are missing, less useful or more expensive (in the sense of cost-to-process) information is substituted, or else changes occur in the procedures so that the perceiver can still construct a reasonable layout of space.

Neither of these alternatives can support research using impoverished environments to test the necessity of a motor component in perceptual processing. A motor component may only be necessary under impoverished conditions, but otherwise is never used. If the visual environment is richly furnished with information, as it is when a perceiver looks at natural scenes under the normal range of daytime or artificial illumination, it may be that visual information alone is sufficient for all aspects of visual perception. As soon as the most useful depth information is removed, however, as it is with nearly every motion-constancy and perceptual-adaptation experiment, then perhaps the only way to disambiguate and integrate the isolated retinal changes is to relate them to changes in one's movements.

In one of the few studies that contrast impoverished and rich information, Lee (1974) reported a series of experiments designed to test gravitational and orientational constancy. In the visually-rich environments the subjects stood in a normal room in which the entire walls and surround of the room could be changed in orientation and even set in motion. Lee found that subjects based all their perceptions and all their judgements upon the visual information around them, irrespective of what their gravitational detectors told them. Such results are in marked contrast to the typical rod-and-frame impoverished scene in which information from gravitational detectors is clearly brought into play (See Ebenholtz (1977) for a review and a model based upon the impoverished testing setting).

Gibson has described in some detail (1966 *op. cit.;* see also Haber 1978) the visual information available on the retinal surface that can distinguish between observer-induced motion and environment-induced motion of all types: saccades, pursuits, head movements, body locomotion, object movement, full-scene displacements, and their combinations. But such distinctions can only be made if the scene is fully articulated in depth. The ground on which the observer is standing and on which objects are resting has to be visible and not empty or textureless. Looking at a flat screen with objects projected on it, or at glowing lines or bars in the dark, could never provide enough information to visually disambiguate observer motion from object motion.

It is possible that sensory-motor interactions are necessary and that an exclusively vision theory of visual perception is inadequate. But at present neither Gibson's claim that this is the case, on the one eye, nor the contrary impoverished-environment evidence, on the other eye, are sufficient to settle the question. Consequently, neither the original H & R experiment nor the Gyr et al. replication, reported here, advance the question at all.

My comments should not be taken to mean that observer motion might be irrelevant for vision. One of the most important sources of information about the layout of space arises from motion parallax and from motion perspective more generally. Without observer motion this information is unavailable. Thus, observers always get more information about space, and perhaps even disambiguate other information, but only if they move. The information acquired in this way, however, is strictly visual and can be interpreted without reference to the magnitude of movement or whether the movement was active or passive. For example, while an observer is fixating on the horizon, his head movements displace the images of all the objects (except those around the particular fixation area) across the retinal surface, with the amount of displacement being inversely proportional to the distance of each of the objects from him. The ratio of the relative displacements is determined only by their relative distances and is totally independent of the source of the initiation of the movement and of the magnitude of the movement. So motion perspective is very useful for visual perception, whether it is passive or active and whether or not its magnitude or direction is monitored.

There are other examples from research on visual perception in which carefully-controlled laboratory studies may lead to wrong conclusions. The past 150 years have produced a magnificent body of work on the effectiveness of different cues to depth and distance. In general, most experiments isolate all but one cue of interest, which is then varied while all others are removed or controlled. Every cue studied in isolation (for example convergence, accommodation, interposition, adjacency, aerial perspective, etc.) has been shown to be effective. Variation in the information from that cue produces variation in perception.

But it is likely that some of these cues are of such low validity that they will never be used when other cues are present. Convergence is probably the best example. The angle between the lines of sight of the two eyes is an obvious logical source of information about the distance of the object being fixated. Gregory (1966) describes convergence information as the input to a human range-finder computer. But as Ogle (1962) has pointed out, registration of convergence is slow, it is imprecise, its range of even minimal accuracy is only for very nearby objects, and most important, it appears to be ignored entirely in the viewing of visually-rich scenes. Welch (1978) has also reviewed data to show that in visually-rearranged environments, where retinal information is pitted against convergence information, it is convergence that is recalibrated. Hence, if convergence is the only source of information available, flexible perceivers will be forced to use it. But as soon as they have other and better information, they pay little attention to convergence.

Thus, while well-controlled laboratory studies, proceeding one variable at a time, sound like good science, they may only tell us what perceivers can do when pushed to the wall, and reveal little about what they normally do. As Gyr et al. note, visual theories of visual perception are theoretically simpler to conceptualize, and they make far fewer demands on the nervous system for their support. It is possible that the behavior of perceivers reflects this as well, so that they use visual information alone whenever there is enough of it, and only resort to more complex and costly processing when needed.

by **Lewis O. Harvey, Jr.**

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Evaluating nonreplication: more theory and background necessary. Current theorizing about the nature of perception has moved beyond the simplistic S-R formulations popular in past decades. Indeed, the original formulation by Gibson of "direct" perception seems as naive today as the attacks against it. The new theoretical orientation has grown out of information-processing (Neisser 1967) and artificial intelligence (Minsky & Papert 1969). Contemporary theoretical interest has become focused on the nature of the processes that take physical energy (stimuli) and calculate transformations for the purpose of creating internal representations of stimuli (e.g. Powers 1973; Sommerhof 1974), as well as on the processes that store internal representations of knowledge (Kintsch 1974). These internal representations provide the basis for decisions about behavior.

A process is a computational algorithm that, given a set of inputs, allows an output to be calculated. These inputs can of course be both external and internal (i.e. the outputs of other processes). The computational result produced by a process is the *metric* associated with that process. The distinction between a metric and the process that produces the metric is important to make, because the same metric could be produced by quite different processes.

Together, processes and their associated metrics form a theory (Anderson 1978) and give scientists something substantial to test, refute, and argue about. The recent literature abounds with descriptions of processes that build internal representations of stimuli (Lindsay & Norman 1977), that compare different internal representations with each other (Tversky 1977; Krueger 1978), and that make decisions (Krantz 1969; Green & Birdsall 1978). These days few doubt that perception, memory, and behavior are mediated by neural circuitry (whether understood at the moment or not); an additional advantage of formulating specific processes and metrics is that they can be examined for neurological feasibility. In fact, where two competing processes are found to be formally equivalent or isometric, or give equally accurate predictions of empirical data, the test of neurological feasibility may be the only way to resolve the conflict (Anderson 1978). But whether or not a process is described in neurological terms is not in and of itself a strength or a weakness.

The major problem with the paper by Gyr et al. is that it never makes a clear enough theoretical statement of the issues to render them testable, it does not critically evaluate experimental evidence cited in discussion of the issues, and it ignores published experimental findings. The authors start with a general statement of the position ascribed to H & R, that motor and visual sensory processes can interact to produce percepts, and the position of Gibson, that a detailed analysis of external variables in the visual array can predict specific perceptual events. I note that these two positions are not *a priori* in conflict with each other, although the authors then set up an implied conflict by stating the conditions under which motor activity should be assigned *a critical role* in visual perception: "motor output must be shown to be *necessary* to the perceptual process." What is meant by "critical role" and "necessary" is not defined.

Another weakness in the paper is that the review of the literature is little more than a listing of some of the studies that have been cited as supporting the two positions. What I kept wanting was a critical evaluation of the literature relative to the issues. And at the end of the paper the authors draw the rather weak conclusion that although sensory-motor interaction has a lot of empirical support, perhaps Gibson's position is not so bad. The basis for this statement seems to be the author's failure to replicate the findings of H & R, since they make no critical or specific analysis of the other evidence.

Unfortunately, the current study does nothing to clarify the issues, nor does it clarify the failure to repeat H & R's results. A replication that obtains results in agreement with the replicated experiment has no problem. But when a replication obtains results that differ from the original (as is the case here), the authors have an obligation to extend the original result and offer experimental evidence explaining the differences. Gyr et al. did uncover a procedural problem with the H & R study, and they imply that this problem is serious. Indeed, the H & R procedure would have introduced a response bias which, in retrospect, one would want to avoid, but since the interpretation of the results depended upon the difference between the pre-adaptation and the post-adaptation measures, any response bias was subtracted out and could not have accounted for their positive findings. The other suggestions made by Gyr et al. about the effects of attention and the direction of flow pattern strike me as rather improbable. In any case, it is the responsibility of the authors to put their notions to experimental test rather than to leave the reader hanging with an inconclusive experimental finding.

The authors would have done the scientific community a service if they had critically examined the empirical data, and instead of asking which position was correct, to have asked under what conditions motor processes interact with perceptual processes. The evidence that springs to my mind certainly supports a model of perceptual processing that permits an efference copy or corrolary discharge derived from motor commands to influence the perceptual outcome (e.g. Stevens' replication of the classic Mach and Kormueller experiments on perception during attempted eye movements of paralyzed eyes; see Stevens on Roland: "Sensory Feedback to the Cerebral Cortex During Voluntary Movement in Man, *BBS* 1(1) 1978 pp. 163–5), and that this motor-derived information is generated before any movement begins (e.g. Matin 1974). An even more valuable service would have been rendered had the authors formulated the theoretical positions in terms of specific processes and made specific models in an effort to integrate and explain the various data that have been offered as support for these two views. It would then be possible to have a clear and meaningful discussion of data and of theoretical issues in the context of the models.

by **Volker Henn**

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Can the brain be divided into a sensory and a motor part? Based on discrepant experimental findings and a review of the literature, Gyr et al. present arguments questioning whether motor systems can have a decisive influence on sensory processing at all. In this short commentary I will limit myself to discussing some aspects of eye movements.

In neither study were eye movements measured. Humans as well as monkeys usually combine eye and head movements, but they will increase the size of saccades if the head is fixed. Concerning the orientation of the prism and the resultant vertical or horizontal displacement, there is no good argument for assuming that the fastest or most effective adaptation occurs to the stimuli that lead to the largest displacement. Another point to consider is that we make fewer and smaller pure vertical eye movements than horizontal ones spontaneously. In the active-vs.-passive-movement paradigm, with each step during the active condition there is some vertical head movement, which induces eye movements via the vestibulo-ocular reflex. Why do we adapt to unusual patterns of sensory stimulation? Conflict between inputs is certainly one possible reason. Therefore, instructions or prior knowledge of the details of the experimental set-up seem to be important. S's mental set may play a role: is he willing to accept the environment as it is? Is he expecting some conflicting cues for which he is eager to compensate?

Turning now to the theories reviewed, a distinction between sensory and motor function is drawn with some effort. Ever since Descartes introduced this sharp distinction, there has been some heuristic usefulness to it. Recent neurophysiological experiments, however, cannot support such a sharp separation. In the vestibular nuclei, for example, secondary vestibular neurons respond differently to vestibular stimulation, whether animals are allowed to exhibit nystagmus or whether they are rewarded for suppressing nystagmus (Buettner et al. 1978). These are cells that are just two synapses away from the hair cells in the semicircular canals. In the superficial layers of the superior colliculi, cells behave differently, depending on whether a target moves across a receptive field, or an eye movement of equal velocity sweeps across the stationary target (Robinson & Wurtz 1976). With such experiments in mind it becomes difficult to decide where the frontier between sensory and motor systems is. There seems to be a multilevel transformation between sensory input and motor output, with feedback pathways at all levels. Trying to avoid complex sensory-motor interactions in experiments is certainly legitimate in order to keep numbers of parameters to a minimum. But a theory or model based on such experiments always reflects such limitations. To generalize from such a model can be dangerous. Although we can perceive while motor output parameters are kept constant, this can never prove that a powerful influence from the motor system upon perception could not be present under different experimental conditions.

Pursuing this question further, Gyr et al. discuss several experiments, starting with flies and fish, showing that these animals cannot compensate for inverted visual input (head or eyes rotated by 180°) with motor output. True, but these experiments bear no relation to human psychology. Humans wearing reversing prisms do reverse their vestibulo-ocular reflex and optokinetic response (Melvill Jones 1977). Cats and monkeys also do so. This is the more remarkable, since the vestibulo-ocular reflex is phylogenetically a very old one and is otherwise elicited so reliably that a failure to do so has been accepted by neurologists, along with other criteria, as a sign of brain death. It is a three-neuron reflex, but it can still be modified, and even inverted. The inverted reflex leads, in turn, to a return to stable visual perception.

Considering optokinetic input once again, if a human subject is put inside a rotating optokinetic drum with such accelerations calibrated so that no conflict arises with vestibular input, humans, too, will *always* perceive circular vection – that is, self-motion – and will perceive the drum as being stationary. Therefore, although the human has so much in common with the fly that he experiences self-motion under these conditions, he can nonetheless adapt with respect to his perception and motor response if he wears reversing prisms [cf. *Vonèche*].

Behrens & Grüsser (1978) have recently described a new visual-motor interaction phenomenon. Making a slow eye movement across a stationary repetitive visual pattern can induce the illusion of pattern movement. The illusory motion perception induces an ocular following movement, which in turn induces the illusion.

Gyr et al.'s review goes on to examine the question of "whether organisms are in fact able to monitor their own motor behavior at a central level." This seems to be a strange question, unless one considers the human brain to be a simple reflex machine. Signals about single eye movements can be reliably recorded in different brainstem areas approximately 100 msec before the movement occurs. Does the brain make use of such information? Yes, because some patients with very recent oculomotor palsy complain that when eye movements are attempted in the direction of the paralyzed muscle, there is a sudden shift of the visual world. With vision restricted to the paralyzed eye, inaccurate visual location (e.g. finger-pointing at objects) will persist for a long time, showing that it is not easy to override such a central signal [cf. *Roland*].

Commenting from the neurophysiologist's viewpoint, in physiology it has taken a very long time to accept that normal motor activity or information-processing from sensory inputs is far more complex than laboratory experiments indicate. Instead of trying to keep all parameters but one constant, experimentors should try to explore one problem under as many *different* controlled circumstances as possible. This leads to the general question: Can we understand complex problems by singling out separate aspects and investigating them either in isolation? or in more primitive animals? or is it *necessary* also to investigate these problems under conditions of complex interaction, as different and more variable information-processing strategies may be involved?

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Is there curvature adaptation not attributable to purely intravisual phenomena? Gyr et al.'s experiment is an important one, for reasons that go beyond his discussion. The theory that the space we see is built of nonspatial visual sensations, endowed with spatial qualities by the effects of motor acts, is an old and sturdy one. The most important component of this theoretical complex is the hypothesis that visual direction (i.e. two-dimensional space) is a function of memories of (Lotze 1965) or readiness for (Festinger et al 1967 *op cit*) tthe movements that are needed to touch or to fixate particular places in the visual field. Direct evidence is scant and contradictory.

Research on sensory recorrelation (e.g. the effects of adapting to distorting spectacles) has provided one source of support, but most experiments in this area demonstrate only a change in the relationship between seen objects and felt directions. Such change is necessarily ambiguous as to whether visual space, sensed body position, or only the correlation between them has changed (Walls 1951; Harris 1963; Hochberg 1963). Only *intra*visual changes, such as changes in apparent curvature or shape, could provide convincing evidence of change in visual space itself (Hochberg 1963).

Precisely that evidence of change in visual curvature was provided by the H & R experiment. We disagree with Gyr et al. and with others who have argued that the prism arrangement in that experiment—i.e., bases oriented either to the right or to the left—provided distorted visual feedback only with vertical head movements. Forward locomotion while wearing such prisms results in characteristic distortions of the optical expansion pattern as well as the eye movements needed to track or to fixate any particular point in the field during the locomotion itself. The H & R experiment would certainly appear to be a valid test of the dependence of visual space on visuomotor habits or readiness. It is the only experiment demonstrating prism-induced curvature adaptation and after-effects in which extended lines that might give rise to the purely visual Gibson normalization effect (Gibson 1933 *op. cit.*) were excluded. Gyr et al.'s failure to replicate the results of that experiment are therefore noteworthy, considering the theoretical load it carried.

The only other experiment bearing on this point, of which we are aware, is one by Miller & Festinger (1977); in that experiment the subject had to make straight horizontal eye movements in order to fixate a point on a curved line that was presented on a gaze-contigent cathode ray tube display. Despite nearly perfect acquisition of the new visuomotor behaviors demanded by this task, change in the measured apparent curvature of the line was unrelated to the motor changes.

The empirical question of whether and when there occurs curvature adaptation not attributable to purely intravisual phenomena (i.e. the Gibson effect) is now a theoretically very important one.

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Visuomotor experiments: Failure to replicate, or failure to match the theory? The paper by Gyr et al. raises two main points:

1. The so-called sensorimotor theory of perception. There are in fact many theories claiming that perception is not independent of motor activity, but very few (if any) claim that motion, or even self-motion, is the only way to give rise to perception (i.e. the subjective experience of the outside world). My own understanding of this problem is not that perception is produced by movement, but that movement is part of the perceptual process. The perceiving subject makes assumptions about external events—assumptions that he verifies through action. The external world can be seen as a flux of sequential events with causal relationships. During perceptual development the predictive nature of these sequences is progressively established. The external world becomes, for every subject, an "assumptive world," which determines his own perceptual experience (Ittelson 1960). Hence, the actual significance of a given external event will only be revealed through the available consequences of the resulting action (i.e., through the possibility of verifying the prior perceptual assumptions about the event.)

Perceptual conflicts may produce a mismatch between the prior assumption and the subsequently experienced result of an action. The "error" observed during action is a cue for elaborating a new set of assumptions. This adaptation process would correspond to a progressive change in the subjective probability of the perceptual assumptions in a given situation. The heuristic value of conflict experiments comes from the fact that they represent an extreme case of normal perceptual conditions. My suggestion is that even in the normal situation the external world is always affected by a probability factor, and that active verification is always required. One exception, however, may be the situation of overtraining, in which the subject may rely more heavily on his assumptions.

These speculations may give some substance to the rather vague "complex interaction" between sensory processes and motor responses postulated by Held & Rekosh (1963 *op. cit.*). The methodology of Held's group in their visuomotor adaptation experiments implies an absence of any error-correcting feedback from movement during visuomotor conflict. In other words, the subject does not have the opportunity to set an external goal for his movement—that is, to make an assumption about the spatial location of the goal—and to compare it with the position of his arm at the end of the intended movement. Another suggestion, corollary to that of the preceding paragraph, is that the error-correcting feedback that exists in most natural situations is key information for the adaptation of behaviour to external events.

The methodological assumptions of Held's group in the eye-hand adaptation studies in fact conflicts with those implied by another set of experiments by the same group, in which the notion of error-correcting feedback is explicitly introduced (Hein & Held, 1967).

2. The H & R experiment. The limited failure of Gyr et al. to replicate the H & R results should not be considered as a failure of the theory. There are many other results from Held's group (and from other groups as well) showing greater efficacy of active as opposed to passive movement in producing visuomotor adaptation. However, further to what has been said above, the mere inspection of one's own moving arm without error-correcting feedback always produces smaller effects. It might have been of interest to compare the results of the present replication with a parallel study using a different kind of exposure (i.e. one involving corrective feedback).

Another more technical point may account for the failure to replicate. In this type of study subjects are often selected on the basis of their ability to adapt to visuomotor conflict. Gyr et al. could have attempted to compare their 7/18 positive adaptors with those of H & R. It is not certain that the range of after-effects obtained with these seven subjects would have been very different from the low but consistent effects obtained by H & R.

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Motor-sensory feedback formulations: are we asking the right questions?

Gyr and his colleagues would have us confront anew the evidence for assigning a critical role to motor activity in visual perception. While their discussion of "sensorimotor processes" suggests a tightly-coupled relationship between perception and action systems, we believe that the authors present a potentially misleading picture of the relationship between efference and afference. The thrust of this commentary will be to lay out some of the logical problems associated with a theory that utilizes the concept of efference copy. By and large, these supplement points already raised in this journal be a number of commentators on a paper by Roland (1978). The present position is that efference copy and its often synonymously used affiliates, corollary discharge and central monitoring of efference, are, with perhaps a single exception, low in theoretical power. This is the *general* claim to be made here. In addition, we wish specifically to point to an alternative account for the type of data that Gyr et al. seek to explain. This focuses on the concepts of information discordance and allocation of attention, which, when allied, seem to provide an adequate explanation of much of the adaptation literature without resorting to unique contributions from efference copy.

Gyr et al. present the classical data for the role of efference in visual perception. Many of the methodological problems in extending this approach to human behavior have been raised by Shebilske (1977) and will not be re-enumerated here. More damaging, however, is the elegant rationale by Turvey (1977a; see also this Commentary and elsewhere in this issue) that an explanation of visual perception, relying on a comparison of efferent signals to eye muscles and the retinal input provided by vision, falls sadly short when we move beyond the situation of a simple eye movement in a stationary head on a stationary body. When one considers the complexity of the visual array (when an individual performs locomotory activities, for example), a simple computational explanation no longer suffices.

It is clear that Gyr et al. wish to extend the efference-copy notion to movement coordination in general. They are, of course, not alone in this enterprise, in that the efference-copy concept is often used to explain, among other things: 1) the superiority of active over passive movement perception (e.g. Kelso 1977; Teuber 1964 *op. cit.*); 2) the ability of subjects to make rapid error corrections in step-tracking tasks well within the bounds of peripheral feedback loop times (e.g. Higgins & Angel 1970); and 3) the motor performance of de-afferented animals (e.g. Taub 1977). While such data require satisfactory explanation, we do not want to place our money on an all-encompassing efference-copy/reafference relationship. As long ago pointed out by Bernstein (1967), there is an equivocality between motor commands and the effects that they produce. There can therefore be no direct comparison between efference copy and reafference, because such a one-to-one mapping between the two sources of information cannot exist.

More important for a theory of coordination is the issue of how the multiple degrees of freedom of the motor apparatus are regulated. Powerful arguments can be generated against a view that efferent commands specify the states of individual muscles. This would result in an extraordinarily detailed efference copy that fails to take advantage of the intrinsic organization of the nervous system (for details see Grillner 1975). Rather, we wish to view efference not in an executive role, but as an *organizational* factor, in which the entities regulated are coordinative structures (Easton 1972; Turvey 1977b)—that is, functional groupings of muscles constrained to act as a single unit.

A specific operation of efference in this perspective is feed-forward in nature, such that the performer is prepared for the impending motor output and the afference arising from such activity. Thus, various experiments have illustrated postural adjustments and descending biasing influences on the segmental machinery in preparation for particular types of activity, such as lifting the arm or dorsiflexing the foot (see Kots 1977). Note that efference does not necessarily carry a central, motor-to-sensory corollary-discharge connotation (Teuber 1964 *op. cit.*). Such a view, while placing the motor commands in a sensory "code" readily available for comparison with reafference, is just as subject to the mapping-invariance and degrees-of-freedom criticisms outlined above. Rather, efference may be viewed in terms of feedforward, which, because of its particular biasing or tuning operations on the spinal cord, constrains the performer to a limited set of activities (Fowler 1977; Greene 1972).

Gyr et al. refer to deafferentation research as evidence for autoregulation of behavior at a central level. In agreement with Pew (1974), we would have to say that the argument is really one by default, taking the following form: 1) peripheral feedback has been eliminated; 2) the animal can perform various motor activities; 3) therefore some internal monitoring mechanism is responsible. A variety of alternative conclusions have been offered (e.g. Adams 1976; Schmidt 1975). But it has never been clear in this formulation what is meant by *monitoring*; or the nature of the entity that is being monitored. Taub's more recent work on perinatal deafferentation (e.g. Taub 1977 for review) can be interpreted to mean that residues of past experiences, efference copies, and the like are unsuitable candidates for the monitored representation. These are likely to be very impoverished indeed and hardly able, even if one could image them to do so, to contain all the details of the action patterns, such as climbing, hanging, and grasping, that have been observed. But the stronger criticism here is that it is a conceptual error to pose the question: Is an efferent signal necessary or not for normal perception? The tight coupling between efference and afference demands that we not treat them as individual entities but rather seek to understand the nature of their interaction.

Some headway has already been made in this regard. There is neurophysiological evidence that, prior to and during voluntary movements in cats, afferent information in the dorsal-column medial lemniscus is modified (Ghez & Lenzi 1971; Coulter 1974). Similarly, anatomical evidence reveals that descending pyramidal fibers exert both pre- and postsynaptic influences on the transmission of sensory information in the spinal cord (Kostyuk & Vasilenko 1968). Furthermore, human psychophysical experiments on the perception of vibratory stimuli show that the sensory threshold becomes elevated during voluntary movement (Dyhre-Poulson 1975). This modulation is specific to the digit being moved and is not merely a general gating effect on sensory inputs. In sum, we have evidence from a variety of sources illustrating the efferent modulation of afference.

Just as interesting is the rather direct influence of afferent information on efferent activity. At a neurophysiological level, Easton (1972) has shown that stretching the vertical eye muscles leads to facilitation and inhibition of cat-forelimb flexor and extensor muscles. A downward-directed gaze results in facilitated forelimb extension while upward gaze facilitates flexion. More recently, Thoden, Dichgans, & Savidis (1977) have produced evidence that hindlimb flexor and extensor activity can be modulated by both vestibular and visual stimulation. Of particular note is the finding that direction-specific reflex excitability in extensor and flexor motoneurons can be induced by rotating a visual display about the cat's line of sight. Thus, counterclockwise rotation, indicating displacement to the right, leads to an enhancement of extensor motoneuronal activity and a depression in flexor motoneurons, while clockwise rotation has an equal but opposite effect. Analogous findings are available from the elegant "swinging room" experiments of Lee (1978) and his colleagues. Even though the subject is supplied with veridical kinesthetic receptor information that the floor is stable, posture and balance are shown to be under visual control, as evident in the excessive sway observed when the room is moved. Indeed, body sway can be visually driven by oscillations as small as 6 mm without the subject being aware of it. All this points to a tight coupling—a specification, as it were—of efference by afference.

The general claim here, then, is that the efference-copy construct cannot handle the vagaries of the motor system, nor does it provide a particularly useful explanatory device for visual perception. Neither do we want to approach the issue of adaptation via a framework that promotes a dichotomy between efference and afference, as Gyr et al. have done. In actuality there is no need to revert to a recorrelation formulation for an explanation of perceptual adaptation. It is now well-documented, for example, that adaptation can occur without movement (Howard, Craske, & Templeton, 1965 *op. cit.*) in passive conditions (Melamed, Halay, & Gildow 1973) and in conditions where passive movement is induced by vibration (Mather & Lackner 1975). All that is needed for adaptation to occur is a discordance between two or more sources of information that are normally congruent with each other. The performer's attempt to nullify this discordance, and hence return the inputs to their previous correspondence, is seen to be representative of the adaptive process. Numerous studies support this viewpoint (see Kornheiser 1976 for a review) by showing that the degree to which adaptation takes place is a function of the information available to the subject regarding the altered state of the system.

While the notion of discordance is plausible as an account for the occurrence of adaptive change, it lacks predictive power with regard to the exact form that such change will take. The additional concept of attentional allocation provides a potential solution to this problem, in that the outcome of any noncorrespondence between two sources of information (say proprioceptive information detected visually and proprioceptive information detected by joint, muscle, and tendon receptors) can be predicted on the basis of the attentional demands of each

input. Thus Canon (1970), Kelso, Cook, Olson, & Epstein (1975), and more recently Warren & Schmitt (1978) have all shown that adaptation takes place in the modality that is not used during the exposure period. When allocation of attention is left uncontrolled, the dominant modality (in most cases, vision) will remain stable, while the paired source of information will undergo an adaptive shift.

We are accordingly left to explain, within this formulation, the consistent finding that self-produced movement facilitates the adaptive process more than passive movement. Viewed from the informational account, we would argue that under active conditions S is sensitized to pay attention to the discordance between the seen and felt positions of the limb, while under passive conditions, attention is more evenly distributed between the two sources of information. Given the dominance of vision and S's inherent bias to attend to it (Posner, Nissen, & Klein 1976), we would then expect greater adaptation under self-produced movement conditions. Hence, what matters for the adaptive process is information about discordance, which, when combined with attentional factors, seems adequate to explain the findings attributed to motor-sensory mechanisms.

In the present view there is, therefore, no urgent need to reopen this issue based on Gyr et al.'s failure to replicate H & R. Many of Held's predictions have been tested over and over again in an area already burgeoned with empirical data (e.g. see Kornheiser 1976; and Welch 1974 *op. cit.* for reviews). The real need is not for more experimentation, but rather for more *understanding* of the nature of the adaptive process, with particular reference to the interaction of efference and afference.

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by **Ivo Kohler**

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A provisional sensory/motor "complementarity" model for adaptation effects. After an impressive amount of experimental research on the phenomenon of adaptation and re-adaptation, occasionally called recalibration, recombination, re-arrangement, re-adjustment, and so forth, the moment for a more rational pause had to come. The Gyr et al. study provides this in a very valuable way.

From the point of view of our earlier Innsbruck studies, we did not find any reason to deviate from a basic theory of direct visual perception in considering general adaptation and re-adaptation processes or the special cases of prism experiments, although in many cases motor activity was clearly coupled with the sensory effects in question. The "complexity" of re-adaptation, as we suggested, resides in the unusually long time that visual input remains "distorted" after prisms are removed. A variety of contextual contingencies are operative during re-adaptation to determine its speed and course. In our studies the pattern appeared to approach the classical conditioning story: After frequent prior presentation of a stimulus configuration to a sense organ under certain characteristic conditions, those particular conditions lost their "neutrality" and became cues for the adaptation effects, irrespective of whether the conditions were "motor" or "sensory." In the case of prism-induced color fringes, for instance, the cue for adaptation to color was the direction of the brightness gradient of the contours in the visual field itself (a predecessor of the well-known McCullough effect). In the case of apparent movement, however, various types of locomotion, combined with head, trunk, and body movement, functioned as the special cues for stabilizing the initially-experienced "textural flow."

Conditional processes of this sort seem to serve as generalized descriptions of the phenomena in question rather than as explanations. Nevertheless, it may be fruitful to adopt an oversimplified "complementarity" model, for the moment, leaving it open as to whether a particular phenomenon should be explained by purely sensory effects (visual or kinesthetic) or by a kind of sensorimotor link. Let me pursue this a little further.

First of all, there exist some noncontingent adaptation (and re-adaptation) phenomena that seem to occur completely independently of any accompanying motor activity, neither active nor passive, other than keeping eyes open, being seated in a chair in the lab, looking through a hole at a target, and pressing a button at the right moment. I suspect that because the situation remains completely unchanged under such conditions, the phenomena obtained look purely "sensory," with no particular "cue" for the attendant adaptational process. In addition, the testing situation is kept identical to the training situation, a point of no small importance, as we shall see later on.

The added "complexity" in the Gyr et al. study may, at first glance, be thought of as the effect of the systematic introduction of motor activity (locomotion, eye, head, and body movements) into the training situation, resulting in the perceived visual gradient changes. The latter effect would have served as a critical one, not only in the case of the "frozen" environment of random spots on the wall of H & R's experimental cylinder, but even in a "living" environment consisting of, say, randomly-moving dots comparable to a swarm of flies, or the snow showers on the screen of a television set. What is true of all these cases when one is moving while viewing them through prisms is the peculiar change of the configurational flux, which diverges from a lifetime of pre-experimental experience. It is this superimposed change that seems to operate as the higher order "stimulus," not the kind or size of the configuration itself.

So far this only describes one aspect of the antecedent training situation. The most important variable in the work of Held and his associates is the question of sel-induced versus imposed activity. This seemed to be the critical factor in determining adaptation effects in a variety of experiments.

It is my personal belief, derived from some of my own observations while wearing various experimental prisms, that a more thorough analysis of pre-experimental life situations may provide the key to a better understanding of adaptation. Consider that most organisms are self-locomoting; thus, in the case of active movement, they are the causal sources of a special group of stimulus transformations superimposed on their own sensory inputs. The condition of passive transportation, on the other hand, occurs rather rarely—indeed, even artificially. Although various types of vehicles now multiply the situations of passive transportation for human beings, nevertheless, a rolling pedestal (as in some of the Held studies) remains a very unusual situation for a healthy man. I should wonder whether experienced wheel-chair riders (especially passively-moved ones), or persons with extensive escalator experience, would have shown the same minimum effect of re-adaptation when wearing wedge prisms?

From such a naturalistic point of view one would expect a rather different result with up/down prisms. A distortion of distance and shape with respect to the ground we walk on causes a much more dangerous change than the deformation of vertical shapes. We have not used up/down prisms because of the highly attendant danger, especially when going downstairs. The same type of transformation from a methamtical point of view, due to the same optical device, may nevertheless be connected to very different "biological" effects, due, for example, to the asymmetry of the pull of gravity.

A personal observation by Taylor (1962) provides a further illustration. Crippled since the first years of his life, he was strongly handicapped in walking. He thus spent many hours a day in a chair, only occasionally standing up to get around his work table. While wearing wedge prisms (base-left), he soon became aware of a decrease in the bending effect and, especially, of the apparent incline of the surface of the table and of nearby areas on the floor. After one or two weeks of such training (four to seven hours a day) the effect became almost "regional," in the sense that it seemed to become linked to the accustomed life situation of sitting and writing at his table; in the case of walking about, the floor appeared almost completely horizontal, but only within the range of his walking cane. Outside this mysterious circle the surfaces continued to appear shifted, and the (vertical) edges bent. This observation and similar ones underscore the importance of equating the training and testing situation.

Some further observations strongly support the existence of motor effects in adaptation (or re-adaptation) (although not their necessity). Eyeglass wearers must often push their spectacles back in place when they slide down the nose. Associated with this active "correction" is a small perceptible jump of the visual array (in the case of myopic lenses, ipsiversive with the motion of the frame; in hypermetropics, contraversive). If habitual wearers instead move empty eyeglass frames up and down, they see clear-cut apparent motion of the visual array (in the direction opposite to the habitual one). But if another person performs exactly the same movement for them, no apparent movement occurs (see Figure 1). I think a

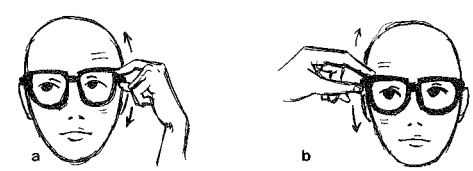

Figure 1 (Kohler). Eyeglass correction: a-active, b-passive. (Artwork by Judith Economos.)

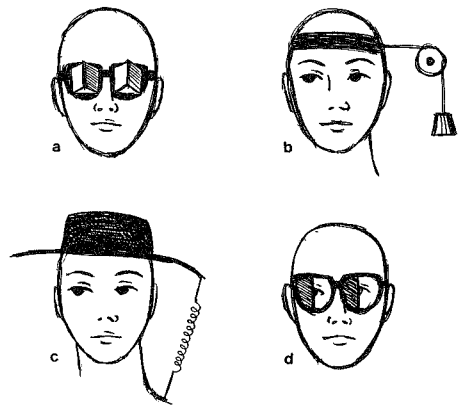

Figure 2 (Kohler). Perception of the visual median. (Artwork by Judith Economos.)

sensorimotor theory in the sense of Held and, more recently, of Hay & Goldsmith (1973) could not be better supported.

An observation with opposite implications (except with respect to brightness, color, and some kinesthetic adaptations) comes from the apparent stability (lack of vibration) of the visual array when one is sitting in a moving car and looking out of a side window. The experience is completely altered if one attempts to observe the image of the landscape as reflected from the inner side of the window on the opposite side. Now, not only does the same visual scene appear to be moving in the wrong direction, but the image is unstable and vibrating. Now let the observer be an experimental subject wearing a pair of inverting or reversing goggles. In the course of the experiment the vibration effect on the visual scenery, viewed directly, decreases distinctly (as a function of the frequency of that experience). Although the subject is passively transported, the process of re-adaptation occurs.

Finally, I would like to present some ideas for further experiments on the sensorimotor problem. The dependent variable here will be the so-called visual median or the perceived "straight-ahead" point (see Figure 2a). There are many ways to influence exclusively the motor part of the phenomenon besides using prisms. Many decades ago an unusual experiment was conducted by the German psychologist Kleint to examine the effects of the neck muscles on the perception of the visual median (see Figure 2b). To study the same question with mobile subjects, able to walk around for hours or even days, we used the edge of a hat connected to the shoulder of the subject by means of a spiral spring or an elastic cord so that the head is pulled toward the point of attachment (see the arrow in Figure 2c). Another solution is illustrated in Figure 2d. Since one side of the visual field is covered, the head must be turned toward the opposite side in order to see objects located straight-ahead (see the arrow). The effect is similar to that of wedge prisms (see Figure 2a), whose deviation nessitates a corresponding deviation of the position of the gaze and/or the head etc., with the difference that the amount of distortion (rotation) in this case also depends on the distance from the visual target.

No doubt there exist many other ways to study the influence of motor activity on vision in man. The question seems interesting enough to stimulate new experimental approaches as well as improved training and testing procedures.

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The encoding of spatial position in the brain. The article by Gyr et al. addresses an important problem concerning how spatial positions of visual patterns are specified by the nervous system. What code determines the spatial position associated with any given receptor, neuron, or muscle cell in the visual or motor systems of the brain? The aim of this commentary is to provide perspective on the relationship of this general problem to the research of Gyr et al.

Insofar as the principal function of vision is to provide spatial information, an understanding of how the spatial positions of stimulation are specified is fundamental to the understanding of vision. Our understanding of this problem is primitive, however. Present knowledge of the structure and function of the visual system is grossly inadequate to account for observers' achievements in resolving spatial relations. For example, Westheimer & McKee (1977) have demonstrated that under optimal conditions in a vernier acuity task, spatial displacements on the order of one fifth of the diameter of a single receptor can be detected in a moving-stimulus pattern impinging upon about 90 receptors in a period of 200 msec. How can the genetics and development of the visual system ever produce a structure that is arranged sufficiently precisely to provide such information about the spatial organization of stimulation? Similarly, difficult problems are also raised by the visual/motor coordination exhibited in many athletic events. How can the positions of receptors, neurons, and muscles be specified in such detail? We really cannot give a satisfactory answer as to how observers can discriminate straight from curved lines either before or after experience with optically-distorted patterns.

A persistently appealing hypothesis discussed by Gyr et al. has been that visual positions are only loosely specified and are readily modified by feedback from motor behavior. Thus, visual/motor interactions with the environment might be used to continually calibrate the visuospatial position of any given neuron. Perceived shapes and locations of stimuli might evolve from such interactions.

To assess the rationale and support for this idea, two logically separate aspects of spatial position must be distinguished: the *exocentric* positions of the component points of a pattern *in relation to each other* (i.e. the shape of the pattern) versus the *egocentric* location of the stimulus *in relation to the observer*. Though these two conceptions of spatial position must involve at least some common aspects, they are logically different specifications of stimulation, perception, and behavioral performance. These two conceptions are intermixed in the discussion by Gyr et al., however, as they are in much of the literature.

Empirical evidence provides very different support for the hypothesis that motor behavior influences the observer's knowledge about either of these two aspects of spatial position. To my knowledge there is little or no unequivocal support for the hypothesis that either efferent or afferent information from motor activity influences perceived exocentric spatial relations among the components of a pattern. The failure by Gyr et al. to find such effects is consistent with many other experiments in the area, although I can offer no suggestions as to why H & R might have obtained a different result. Miller & Festinger (1977), for example, have convincingly demonstrated the absence of any influence from rearranged eye movements on perceived curvature in what might be considered a more direct test of the same hypothesis tested by Gyr et al.

Evidence on the hypothesis that motor activity affects the perceived egocentric spatial locations of stimuli in relation to the body is more complicated, but many examples of such effects can be found. Most of these involve the positional guidance of motor responses (e.g. of the eyes and hands) by visual stimuli, though the findings have been less consistent and less convincing with more abstract responses (e.g. verbal ones) not physically directed toward a particular environmental location. A variety of phenomena suggest that the brain employs separate systems for controlling the spatial position and movement of the eyes, limbs, and body as opposed to the verbalizable subjective experience of the location of a stimulus. The systems for controlling the spatial positions of the body and appendages appear to be quite plastic and readily modified to adapt to altered relations between visual stimulation and bodily position. Subjectively-experienced egocentric locations, however, appear to be only loosely coupled to these motor control systems and to be strongly influenced by exocentric frames of reference.

Length constraints on this commentary preclude a review of the vast and confusing literature on this problem, but a few examples may be suggestive. Miller & Festinger (1977) found that pursuit eye movements were quickly reprogrammed to adjust to an altered correspondence between eye movements and locus of retinal stimulation; but despite this plasticity in eye-movement control, the perceived curvature of stimulus patterns was essentially unaffected by the changed visual/motor correspondences. Hansen & Skavenski (1977, 1978) have reported that the brain maintains precise information about the positions of retinal loci during eye movements, so that a brief flash during an eye movement may be accurately refixated or located by hand, whereas other experiments have demonstrated that subjectively-experienced egocentric spatial positions of brief flashes (as judged in relation to subsequently-presented stimuli) are inaccurately and inconsistently influenced by eye movements (e.g. Matin 1972). Finally, Harris (1974) has demonstrated that egocentric judgements of "straight ahead" are systematically biased by external frames of reference, as if knowledge of the relative positions of the body and external stimuli were inaccurate, although the skillful visuomotor coordination exhibited in athletics indicates very precise egocentric localization. In sum, it is difficult to avoid the conclusion that control of the positioning of eyes, limbs, and body is more accurate than the subjective experience of egocentric position. The plasticity of subjective egocentric spatial

position is unclear, but this conception of spatial position seems to be strongly influenced by exocentric frames of reference.

Questions about whether and how motor activity influences perception are entwined with conceptions of the organizational interactions between sensory and motor subsystems of the brain. Traditionally, these have been implicitly considered as two discrete subsystems, connected at only one main junction between an implicit "sensorium" and a hypothetical site for initiating voluntary responses. If the afferent systems were isolated in this way from the efferent systems, then analysis of the locus of perceptual learning might be relatively straightforward. It would be appropriate to ask whether changes were visual, proprioceptive, motor, and so forth.

However, an alternative conception suggested by evidence on the varieties of spatial representation in the brain could consist of multiple, partially-coupled, and nested feedback-control systems, involving multiple spatial reference systems. Sensory-motor interactions probably occur in many different ways, depending on the particular tasks to be performed. Perhaps it is not sufficient to ask whether "motor" activity influences "visual perception," for these may not be unitary processes. Instead, we might ask how sensory and motor processes are integrated in representing spatial positions for the performance of various activities.

Parenthetically, J. J. Gibson's approach seems more compatible with this latter conception of perception—as an implicit aspect of interactions with the environment—rather than the narrower characterization given by Gyr et al. (See Mace (1977) for an excellent discussion of the breadth and implications of Gibson's approach.)

by **Arien Mack**

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Non-Visual Determinants of Perception. There are a host of reasons why the question of whether perception is determined by non-visual as well as visual factors cannot rest on whether or not there is perceptual adaptation to an imposed curvature distortion. Let us briefly consider two of these reasons. First, despite the many theoretical differences among investigators, there has been almost unanimous agreement that adaptation to curvature distortions is, at best, minimal. Both Held (1968) and Rock (1966 *op. cit.*), who otherwise have sharply conflicting views about the nature of perceptual adaptation, have argued that adaptation to curvature distortions, unlike adaptation to rotations or displacement of the field, may be inherently limited. Why then choose curvature as a means of investigating the questions of the nonvisual or sensorimotor contributions to perception?[1]

Second, as the authors correctly point out, the principal case for the contribution of motor factors to perception has been made by the work of Von Holst & Mittelstadt and Sperry, cited by the authors. This work is directly related to the phenomenon of position constancy, perceiving that objects in the visual field appear stable despite the movement of their images over the retina caused by movements of the observer. It is the literature on position constancy and the adaptation of position constancy that is, I believe, the literature most relevant to the question of whether there are motor determinants of perception. The literature in this area makes very clear, not only that position constancy is a robust phenomenon (Bridgeman et al. 1975; Stark et al. 1976; Mack & Herman 1978; Mack 1970), but that the adaptation of position constancy occurs (Wallach & Kravitz 1965a), occurs rapidly (Wallach & Kravitz 1965b), and is completely dependent for its occurrence on movements of the observer. It is therefore an exemplary case of the involvement of motor factors in perception, since this adaptation cannot occur unless the observer is moving. The adaptation of position constancy involves a recorrelation between motor factors, the observer's head or eye movements, and visual factors, the rate, extent, or direction of image movement contingent on movements of the observer.

Gibson and his followers (see Lee 1974) have tended to explain position constancy in terms of what they call "visual proprioception." Because the total displacement of the visual field is invariantly related to movements of the observer, and not with movements of objects in the field, it is argued that this kind of image displacement always signifies observer, not object, movement. Similarly, relative displacements within the retinal image are invariantly related to object motion and thus signify movement in the external world. Gyr et al. point out that Gibson attempts to deal with the Von Holst & Mittelstadt and Sperry findings in much the same way that he attempts to explain position constancy. This explanation, however, cannot account for a corollary of position constancy—namely, that an afterimage viewed in complete darkness, or a moving object accurately tracked by the eyes and viewed against a homogeneous ground, appears to move. In fact, in the case of the afterimage its apparent movement closely parallels the motions of the observer's eyes (Mack & Bachant 1969). In neither instance is there any image movement, total or relative; nevertheless, object movement is perceived. These situations present no problems for theories of perception that allow for motor determinants. They are accounted for in terms of the presence of eye-movement information and the absence of image displacement. This mismatch leads to the perception of object movement just as inevitably as the match between observer and image movement leads to the perception of position constancy. These instances are, of course, what Gibson might describe as minimal-stimulus situations, possible only in a laboratory, but that interpretation merely inappropriately dismisses rather than explains these highly reliable events.

To the question of whether there are non-visual or motor determinants of perception, the answer then would seem to be affirmative, but it should also be recognized that there are occasions in which perception is strictly determined by visual input alone. These, in fact, may be considered two separate modes of perception: a subject-relative and an object-relative mode (see Mack 1978 for a fuller discussion of this distinction). All instances in which perception is jointly determined by visual and non-visual (motor) factors would seem to be instances of subject-relative percepts—that is, instances where perceiving is in relation to the observer rather than other objects in the visual scene. This mode of perception may be distinguished from object-relative perceptions, which are strictly determined by visual information only, and where perceiving is in relation to other objects in the scene. For example, the perception of an objects's size may be a function both of its retinal image size and information about the distance of the object from the observer derived from the extraretinal sources of convergence and accomodation. This is clearly a subject-relative precept. On the other hand, the perceived size of an object may also be based on its size relative to an enclosing framework, where distance or extraretinal information play no part (Rock & Ebenholtz 1959). This is an object-relative percept. Similarly, the perception of motion or of the apparent speed of an object may be based on the latter's motion with respect to the self or with respect to other objects in the field. In the first instance the perception is determined by retinal-image motion coupled with extraretinal eye- and head-movement information, while in the second instance the perception is determined by retinal information alone. It is based on the retinal motion or speed of motion of an object relative to its retinal surround, as in the case of the "transposition of velocity" (Brown 1931), in which apparent speed is a function of the rate of relative displacement of an object with respect to its visual surround, rather than its rate of displacement with respect to the observer.

An interesting feature of object-relative perception is that it is frequently in conflict with subject-relative perception and thus represents the overpowering of subject-relative and veridical perception by object-relative and illusory perception. This description characterizes both instances of object-relative perception discussed here. To illustrate: where the apparent velocity of an object is based on its rate of retinal displacement relative to its surround, objects moving at very different rates are perceived as moving at the same rate when they are being displaced at the same rate with respect to their visual surrounds; meanwhile the eye-movement/image-movement information on which the subject-relative percept is based, and which is simultaneously available to the perceptual system, would lead to the veridical perception of velocity.

In summary, to deny that perception is determined by motor factors or to assert that it is always so determined seem to be equally mistaken views. What we must determine is when and why it is one rather than the other.

NOTE

1. There is an experiment by Held (Mikaelian & Held 1966) examining adaptation to field rotation and closely parallelling the Held & Rekosh (1963 *op. cit.*) study. In one condition of that experiment, which also employed conditions of active and passive movement, observers were exposed to prisms in an environment that contained no visible lines, but only dimly-luminous spheres. This was done to control for normalization of tilt and is thus quite analogous to the Held & Rekosh study, which controlled for the normalization of curvature in much the same way. Since adaptation to tilt distortions is known to occur (see Stratton 1897; and Mack & Rock 1968), it would appear to make somewhat more sense to examine the question of sensorimotor contributions to perception in this context, rather than in the context of curvature adaptation (although it will be argued in the text that there is still a far more relevant context for examining this question).

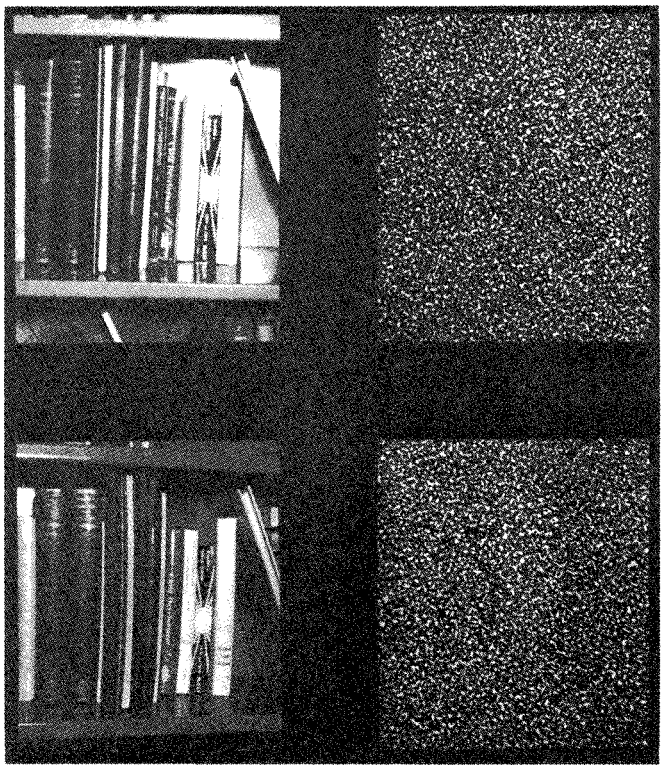

Figure 1 (Mikaelian). The upper pair of scenes are shown as viewed normally, the lower pair as viewed through a wedge prism. The left-hand scene, with its linearly ordered contours, appears curved and distorted by the prism; whereas, the right-hand scene, composed of randomized spots, appears unchanged. (Reprinted with permission of M.I.T. Press.)

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Adaptation ot the distortion of shape is different from adaptation to the distortion of space. The sharp difference between the H & R results and Gyr et al.'s attempted replication is another instance of conflicting results from similar experiments, a situation not that uncommon in prism studies, and one that probably arises from subtle differences in procedural or equipment details that workers fail to report. Gyr et al. offer an elegant and critical analysis of the implications of the H & R study. Held and his co-workers interpreted their early prism studies as instances of the involvement of the motor system in vision, with many of the investigators preferring to use the term "perceptuo-motor" response when referring to the perceptual responses being investigated (such as shape, distance, orientation, localization, etc.). Most of these studies were conducted within a conceptual framework that considered perception to be a unitary process, and it was assumed that adaptation to rearrangement of visual space followed the same rules, whether one considered adaptation to the distortion of shape, spatial localization, or other variables (all induced by wedge prisms).

A major difference between adaptation to the distortion of shape and to spatial localization was evident, however. Prolonged active viewing through prisms produced curvature after-effects that were a small fraction of the prism-induced curvature (Kohler 1964) and comparable to those obtained by passively viewing an array of curved lines (Gibson 1933 *op. cit.*). Full and exact compensation to the visual displacement could, of course, be obtained (Held & Bossom 1961).

The possibility that there may be *two* processes operating in adaptation to rearrangement was discussed in a subsequent paper by Mikaelian & Held (1964), although these discussions were in relation to adaptation to prism-induced visual tilt.

In later papers Held expanded on his formulation of the extent of the involvement of the motor system in the processing of shape (Held & Hein 1967; Held 1970). Along with other investigators (Ingle 1967; Schneider 1969; Trevarthen 1968) he suggested a dual process in the analysis of spatially-distributed stimulation, referring to the dual modes as "identification" and "localization" (Held 1968). Processing of shape information was ascribed to the "identification" mode of stimulus analysis; its processing was more or less hard-wired, its plasticity limited, and its operation dependent upon such cortical units as edge detectors, feature analyzers, and so forth. Beyond a critical period, developmental influences on these processes were said to be limited. In contrast, the "localization" mode of processing, which mediated information such as position relative to the environment, movement of self vs. the environment, orientation or distance in space, and so forth, was said to be highly labile and integrally related to the sensory *motor* system. Held suggested that rearrangement experiments were relevant primarily to the latter category of perceptual responses.

Considering such a dual mode and the conditions that evoke one or the other mode of analysis of spatially-distributed stimuli, this commentator is not surprised that Gyr et al. were unable to obtain reliable curvature after-effects. Stimulus-contour (or texture) density is an important variable in invoking one or the other mode of analyzing the visual array (Held 1970), with impoverishment favoring the locus-specific mode of operation. Gyr et al's experimental condition drastically reduced the relevant reafferent information (due to the low density of viewing contours), which, added to the limited modifiability of form perception, produced the observed results. An illustration of the very high-density random-dot spot field used in the H & R study may be found in Held & Hein (1967). (It is unfortunate that H & R did not publish this information in their original article.) [See figure 1.]

In replicating prism studies, or in designing new ones, useful information can be gained by making a distinction between the dual modes of processing spatially-distributed stimuli. I would hazard a guess that if, in addition to curvature, Gyr et al. had measured egocentric localizations, they would have obtained significant adaptive alterations.

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Visual-motor conflict resolved by motor adaptation without perceptual change. In their closing comments Gyr et al. suggest that the sensorimotor model may be more readily validated for situations in which an experimentally-produced conflict cannot be ignored but must be resolved by the subject. Measurement of *motor* adaptation, which might provide one kind of evidence for conflict resolution, is, unfortunately, absent from both the Held & Rekosh (1963 *op. cit.*) study and from Gyr et al.'s replication. Such measurements have been obtained in an adaptation study by Miller & Festinger (1977), which involved conflict between the shape of a visually presented curve and the pattern of eye movements necessary to scan that curve.

Briefly, the experiment was as follows. Subjects viewed a computer-generated display consisting of horizontally-oriented, concave-up curved lines. The position of these curves was contingent on the horizontal position of the eye so that, in order to scan a curve errorlessly, the eye would have to execute purely horizontal saccades. In one condition this was achieved by moving the curves vertically so that the point fixated always had the same vertical location. Eye movements were reprogrammed rapidly to eliminate the vertical components of the saccades that were present at the start. Thus, subjects did effectively deal with the sensorimotor conflict. There was, however, no change in the perception of curvature in excess of that measured following equivalent viewing of a stationary display (i.e. the Gibson normalization effect). In another condition the eye-position-contingent display was again moved vertically, but in such a way that the vertical components of scanning movements would need to be double what is normal for fixations to be accurate. Again, eye movements were rapidly and appropriately adjusted and, again, there was no perceptual change in excess of normalization. In yet another condition the curves were displaced horizontally so as to simulate the effect of viewing a straight line through a base-down wedge prism on a contact lens. A small amount of perceptual adaptation in excess of normalization was found in this condition, but it was quite unrelated to oculomotor retraining and apparently due to some property of the stimulus situation.

Thus, this experiment implies that, at least with the afferent visual and oculomotor systems, sensorimotor conflict is resolved by altering motor programs without altering either perception or, presumably, afferent visual processing. This position is consistent with that of Harris (1965 *op. cit.*), who concludes that in such conflict situations it is the felt positions of body parts that change, and not visual perception.

It is possible that information based on relative retinal location is essentially unalterable and dominates other conflicting sources of information. If this is true, perceptual adaptation to sensorimotor conflict may only be possible for cases in which such intravisual information is not involved.

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Centrifugal contributions to visual perceptual after effects. Although the purpose of the experiments by Gyr et al. has been to replicate the study by Held & Rekosh (1963 *op. cit.*), there are some important departures.

1. The subjects of the Gyr et al. study were not investigated in the "passive" condition of being wheeled around inside the experimental cylinder, as in the H & R study. The main feature of interest in the H & R study is the distinction between the subjects during "active" locomotion and those during the "passive" condition mentioned above. Moreover, all of the H & R subjects were tested under both conditions. Thus each subject served as his own control. Gyr et al. only tested their subjects during "active" locomotion.

2. Gyr et al. make an important point in the addition of a base-up prism. Their arguments for the use of the base-up prism are reasonable. However, they should still have tested their subjects under "active" and "passive" conditions with both the base-up and base-right prisms.

3. There may be other minor differences in the experimental apparatus used in the two studies that contributed quantitatively to the observed differences in parameters.

This commentator feels that Gyr et al. should have questioned the conclusion arrived at by H & R more critically, rather than their experimental technique. Much of the background literature reviewed by Gyr et al. seems to be concerned with the importance of motor-sensory feedback (resulting from voluntary movement) in contributing to visual perceptual effects. There is no adequate discussion of possible effects due to centrifugal control of the retina (Granit 1955 a,b). It is known that efferent modulation of the impulses of the ganglion cells in the retina may be achieved by stimulation of the reticular formation (Granit 1955a). Stimulation of the same area also modulates the impulses in muscle spindle receptors through the gamma efferents (Granit & Kaada 1952). Thus, the centrifugal effects of visual perception may occur *simultaneously* with voluntary movements as a result of a *common* centrifugal drive, rather than following the effects of the voluntary movement. It is also known that the main feature of such a centrifugal drive to the retina is to produce an inhibition of the receptor, followed by an excitatory rebound when the stimulation of the reticular formation is stopped (Granit 1955a). Thus, the perceptual after-effects may be due to such a phenomenon.

When von Holst & Mittelstaedt (1950 *op cit.*) postulated their "Reafferenzprinzip," the idea of centrifugal control of sensory endings was rather unknown. With current anatomical and physiological knowledge, the Reafferenzprinzip can surely be modified. In fact, current data favor the idea of central nervous system control, not only of the sensory endings themselves, but also of the information transmitted in the ascending spinal tracts at the level of the second-order neurone (Ghez & Lenzi 1971; Ghez & Pisa 1972; Coulter 1974). In psychophysical experiments on human subjects, Dyhre-Poulsen (1978) has shown that the threshold for a vibratory stimulus increased before ballistic movements and during a tracking movement of the vibrated finger. Similarly, the perception of electrical stimuli to the finger-tip may be abolished during an active movement, with a gradual reduction before the start of the movement (Coquery 1978). The changes in visual perception observed in the H & R study are probably due to a similar mechanism.

The discussion of de-afferentation literature in the background analysis is not necessary. In any event, there is some arguement as to whether dorsal root section can effectively produce de-afferentation due to the recent discovery of a large number of nonmyelinated afferents that enter the cord through the ventral roots (Coggeshall et al. 1975; Appelbaum et al. 1976; Clifton et al. 1976).

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Position information versus motor programs: two levels of sensorimotor theory. The lasting significance of the Gyr et al. study will depend upon the reason for the absence of significant adaptive shifts. Suppose that the null results reflect the true state of the world, and that the H & R findings resist replication, even under conditions of exact duplication of dot density, attentional set, method of testing, and so forth. This would suggest that the remarkably consistent shifts reported by H & R in the active condition must be chalked up to sampling error or, perhaps, to uncontrolled exposure to straight-line contours. Even if we do eventually find ourselves in this position, it would seen that the fundamental role of the motor system in a variety of visual phenomena would still go unquestioned. For example, there can be no doubt that the registration of eye-position information contributes to the perception of visual direction (Paap & Ebenholtz 1976), object rotation in either the sagittal or horizontal plane of the observer (Ebenholtz & Paap 1976), and convergence-based distance (Paap & Ebenholtz 1977). Similarly, the effects of registered head position have been shown to influence the perceived orientation of a line rotated in the observer's frontal plane (Ebenholtz & Benzschawel 1977) and the perceived direction of a luminous target presented in the dark (Ebenholtz 1976). All of these examples fit neatly into the invariance-algorithm approach to the visual constancies, simply requiring the visual system to correct the retinal input by taking position information into account. When muscle potentiation or reflexive movements are induced, small departures from constancy commensurate with the error in registered position are observed.

We should probably view the contribution of the motor system to the perception of direction and orientation as qualitatively different from the possible role of the motor system in the extraction of form. One difference is with respect to the time and number of position values that must be used to construct each type pf perceptual attribute. For example, the perceived direction of a point source relative to the median plane of the head requires the registration of a single eye-position value—namely, the position of the eyes at the time the target is presented. Because the required eye position corresponds to the current eye position, it need not be the case that the information comes from an efference copy. In fact, Shebilske (1976) has argued convincingly that visual direction may be mediated by inflow information. On the other hand, for the perception of curvature to be mediated by motor correlates would require the activation of a number of positions integrated over time. If shape is to be resolved in advance of the actual excursions of the eye/head system across the contours, then it must be further assumed that perceived curvature is mediated by efferent readiness. Clearly, a sensorimotor account of shape perception must rely on much more complicated mechanisms than those needed for direction or orientation.

A recent study by Miller and Festinger (1977) supports the view that oculomotor programs may have little or nothing to do with adaptive shifts in perceived curvature. In one condition of this study a computer-generated display is used to mimic the curvature effects of a wedge prism mounted on a contact lens. On-line recordings of the subject's eye position show that oculomotor retraining follows a time course different from that of curvature adaptation and reaches considerably larger magnitudes; for example, after five days ain the 16.7-H (Horizontal Curve Movement) conditon, adaptation has reached a level of only 4 min. of arc, whereas the improvement in oculomtor guidance would predict an effect of at least 10 min. of arc. Miller & Festinger correctly conclude that their results are inconsistent with theories such as those offered by Held (1961 *op. cit.*), Taylor (1962), and Festinger et al. (1967 *op. cit.*), since these sensorimotor theories require a close relationship between motor relearning and perceptual change. The results of the Gyr et al. study, together with those of Miller & Festinger, do seem to bring a serious challenge to the position that stored efferent programs underly the perception of curvature.

We should also consider the possibility that the present failure to replicate reflects a critical difference in experimental design, and that the H & R findings will be replicated when the appropriate missing link is reinstated. Gyr et al. draw our attention to an extremely promising interaction between dot density and attentional set. Epstein (1975) has summarized a number of studies that indicate that allocation of attention may greatly influence cue dominance and, consequently, the locus and magnitude of adaptive changes. He further suggests that the allocation of attention, rather than the special contributions of re-afference, may be responsible for the frequently reported failure to obtain significant adaptive shifts under conditions of passive movement. This argument rests on the reasonable assumption than when movement is active and self-directed, the subject is more likely to process task-relevant information. It is tempting to suggest that the density and configuration of the dots used in the H & R study may have been more conducive to the perceptual isolation of specific sets of dots, and that the active subjects paid attention to the systematic, but aberrent, transformations of those specific sets, whereas the passive subjects did not.

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Attention as an explanatory concept in perceptual adaptation. Replication is perhaps the most powerful but also the most neglected procedure in psychological research. In the face of multiple, unknown, and practically-unknowable variables, realistically-limited experimental control, and necessarily-fallible statistical tests, successful replication is the most convincing evidence of the "reality" and, to a lesser degree, the generality of a result. For the same reasons,

unsuccessful replication is among the more problematical events in research. Short of doubting the ethics of the researchers, which is at least counterproductive, one is left with the noisome task of seeking explanations among the numerous, minute, and inevitable differences between studies, and of constructing tests among the various hypotheses. The very clear failure of Gyr et al. to replicate the findings of H & R is certainly an instance of such a problem. The intent of this commentary is to make a positive contribution toward solution. First, several differences between studies are noted which may be important, but which the authors either did not notice or for which they lack an explanatory rationale. The last part of the commentary constitutes a word of caution against the use of "attention" as an explanatory concept in the absence of a theory of attention.

As Gyr et al. point out, their procedure counterbalanced prism base direction in the test, while H & R maintained the same base direction in the test as was used in the exposure. Therefore, it seems possible that H & R's *test* period might have induced "Gibson effects" that appeared as "adaptation." Also, apparent adaptation could be due to some response bias induced by the constant starting direction. Of course, such artifactual adaptation should also have appeared for H & R's passive group, but perhaps such effects might somehow interact with adaptation to cancel out when test and exposure base directions are different. In this regard, it would be interesting to know if those Ss in the Gyr et al. study who did show adaptation were also the subjects who received congruent base directions during both exposure and test.

H & R made a point of keeping the Ss head stationary and preventing any sight of the body during exposure, while Gyr et al. report no such precautions. To the extent that Ss did move their heads and see body parts, proprioceptive/kinesthetic adaptation could have occurred. There is some evidence of a reciprocal relationship between adaptive components (Redding 1978), such that increasing proprioceptive change is accompanied by decreasing visual compensation. Thus, it is possible that adaptation in the Gyr et al. study was largely nonvisual and consequently did not appear on their test. Also, H & R's precautions could have directed "attention" to proprioceptive/kinesthetic input, causing adaptation to appear in the "nonattended" visual modality (Canon 1970; Kelso, Cook, Olson & Epstein 1975; Uhlarik & Canon 1971). Gyr et al.'s instructions apparently did not include such a "directed-attention" manipulation.

Finally, the exposure environment used by H & R consisted of "small spots of irregular shape" (p. 722), while Gyr et al. used circular, colored dots. Possibly the varied shapes used by H & R induced greater overall vigilance or selective scanning than did the more regular shapes of Gyr et al. Of course, the more actively the S "looks" at the environment, the greater should be the level of adaptation.

The authors suggest that the most likely explanation of their failure to replicate H & R is differences in attention, and several of the above hypotheses also involve the idea of attention. However, the word "attention" should be used cautiously, since it seems to carry a large amount of pseudo-explanatory power. Indeed, in most traditional perception literature there are few instances where "attend" could not be replaced with "perceive" with no substantive change in meaning (Kaufman 1974). In particular, it seems unnecessary and misleading to invoke the idea of attention to explain so-called directed-attention effects. These studies (e.g. Canon 1970; Kelso et. al. 1975) suggest that when two spatial modalities are providing discrepant information about a distal object, it is the nonattended modality that become recalibrated. However, the attentional manipulations in such studies may be more simply interpreted as specifying the information source controlling exposure task performance (see, also, Warren & Schmitt 1978), while the noncontrolling information source (e.g. modality) is subject to adaptive recalibration. With this interpretation, adaptation *must* be restricted to the noncontrolling, "nonattended" modality, since recalibration of the controlling, "attended" modality would disrupt task performance.

Thus, there is a serious question whether the idea of attention adds any explanatory or predictive power beyond that which might be achieved by a careful delineation of situational performance requirements (including instructions). Instructions that specify a controlling modality may be considered simply another task variable, and without a theory of attention, identifying such instructional variables as "attentional" creates an illusion of explanation.

Current information-processing theory includes a theory of attention that might be applied to perceptual adaptation research (e.g. Posner & Snyder 1975; Schneider & Shiffrin 1977). Attention is conceptualized as the regulation of a limited-capacity, central-processing mechanism that comes into play when nonhabitual behavior is required. Available processing capacity may be intentionally directed to a particular task (selection), but when conscious attention must be given to several simultaneous tasks (distribution), processing demands may exceed available capacity, with resultant interference. Thus, in novel situations, information processing is intentional, may give rise to conscious awareness, and may preclude other mental activity. Otherwise, processing is "automatic," not limited in capacity, and without intention or conscious awareness.

Such a theory of attention is capable of objective test and imparts explanatory substance to the idea of attention. However, until such a theoretical position has been articulated for perceptual adaptation, it is best to avoid use of the term attention, since it obscures rather than enlightens, and it may misdirect research effort.

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Re-afference in space and movement perception. Motor re-afference (central) and motor-sensory feedback (central-peripheral-central) both cooperate with vision and hearing as well as with somatosensory information in space perception. Perception of motion in the environment, self-movement, and change in rate of movement are critically dependent upon re-afference. Cell assemblies (Hebb 1949) and phase sequences are established early in ontogeny as neural-event sequences, or they are innately determined (as in the looking response of infants) as integrative mechanisms for appropriate perceptual and behavioral adaptations. These aspects of space perception require exceptionally fine tuning if motor behaviors are not to remain awkward. Sensorimotor correlates of hue, tonal qualities, or odor perception are, by contrast, far less critical.

Clearly, a re-examination and refinement of data are called for in relation to more specific applications of sensorimotor theory. Re-afference and motor-sensory feedback need isolation and individual evaluation. Although difficult, de-afferentation studies have contributed to this and provide some of our best evidence in support of the contribution of re-afference.

The experience of external motion must often be distinguished from that of self-movement by virtue of re-afference. Disturbing perceptual discrepancies result when expected correlations of events fail. An automobile driver misperceives when he presses on the accelerator (or brake) when normal change in speed fails due to malfunction. When the accelerator is ineffective, an apparent *slowing* of the vehicle results. With brake failure the car is felt to increase in speed. These paradoxical effects of re-afference are akin to the familiar example often cited by Teuber: The attempt to move the eyes laterally, if prevented by paralysis of eye muscles, makes for perceived movement in the environment. [See Stevens, on Roland *BBS* 1 (1) 1978].

Within limits, which should be more adequately studied, correlations between sensory events and between motor-sensory sequences are not only possible but absolutely necessary. Bodily growth changes are in themselves going to be disruptive unless re-correlations occur. As psychologists, we are still groping for improved experimental specifications for the conditions and consequences of both variable and constant shifts in the time and space domains of environment.

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The problem of adaptation to prismatically-altered shape. The H & R experiment that Gyr et al. repeat has been regarded as one of the crucial findings in the area of perceptual adaptation. It not only seemed to demonstrate the necessary role of active compared to passively-imposed movement, but it also seemed to elegantly rule out explanation in terms of after-effects or normalization effects from mere exposure to certain configurations. That an observer would undergo adaptation to shape (along the curvature-straightness continuum) without exposure to any such shapes had been a dramatic – indeed, surprising – finding. It was even more surprising, considering that obvious prism effects would be quite limited for an observer wearing base-left or right prisms but moving only horizontally. Prisms in this orientation displace visual objects differentially along the vertical axis as a function of angle of the incidence of light rays. Therefore *vertical* movements of the observer would provide at least potentially usable information about the distorting properties of the prism relevant to curvature in terms of the differential "flow" of images at different vertical positions in the field. But there could hardly have been very much vertical movement from the bobbing of the head during walking movements especially since Ss were told not to move their heads. Ss who were moved passively in a cart may not have moved their heads at all (thus the active and passive conditions may have differed somewhat in the degree of vertical head motion – an uncontrolled variable that assumes some significance in the light of the greater relevance of vertical over horizontal

movement in the experiment). For further analysis of this issue, see Victor (1968 *op. cit.*) and Welch (1978).

To maximize information about the optical effect of the prisms, it would be desirable to place them in a base-up or down position, because then the differential "flow" referred to above does occur with horizontal walking motion. In fact, Victor (1968 *op. cit.*) tested this by comparing the effectiveness of base-up vs. base-right prism orientation and showed very clearly the greater effectiveness of the former condition. But his experiment, unlike that of H & R, was performed in the more typical adaptation environment containing straight contours. At the outset, straight horizontal contours on a wall will, of course, appear curved when viewed through base-up or down wedge prisms. But during movement parallel to such contours, the region straight ahead will always appear at the same elevation. Thus, information is available that the line is horizontal and straight. Had the H & R experiment been done with base-up or down prisms, the information would not have been this direct, but the up-down flow of images of spots, if interpreted by the perceptual system to be the result of observer motion rather than object motion, could at least conceivably have provided indirect information about curvature.

The results of the Gyr et al. study thus leave us with several mysteries. Why did they not obtain any significant adaptation when the only changes in procedure from that of H & R, as far as one can tell, were trivial (e.g. dot density on the surface of the drum)? Only about half of their observers showed a shift in the predicted direction. (Given this finding, there is no possibility of expecting any difference between active and passive conditions, which is why, I take it, the investigators did not even bother to run a passive condition.) Or is the real mystery why it is that H & R obtained adaptation in the first place? A second mystery is why Gyr et al. did not obtain any adaptation, even in their base-up and down conditions. Or is the answer to this question that the indirect information provided by differentially displacing spots is simply not adequate for adaptation to contour shape?

Let us assume that what is important for adaptation of the kind under discussion is available information concerning how the optical device distorts or otherwise alters the retinal image. Then, if no experiments had yet been done on this problem, it would be plausible to predict that adaptation to prismatically-altered curvature would occur if the following three conditions held: 1) The observer moves around during the prism-exposure phase (or, perhaps alternatively, objects are moved around). Without such movement it is difficult to imagine how any information concerning the prism distortion would be available. Passive movement might suffice, as long as the observer appreciated the direction in which he was moved (again, see Victor 1968 *op. cit.*). 2) Straight or, for that matter, curved contours as well, are visible in the scene. 3) Observer movement is parallel to the axis of curvature distortion rather than orthogonal to it. Given these suggested preconditions, the Gyr et al. negative findings are not surprising at all, since precondition 2 is not fulfilled; but the H & R positive findings would indeed be surprising, since preconditions 2 and 3 are not fulfilled. It would obviously be important now for Held himself, or others, to re-run this kind of experiment, so that we can at least be sure of the facts.

But perhaps the most important mystery of all about perceptual adaptation to altered shape – not touched on in the Gyr et al. paper – is why it is so slight (a matter of a few diopters only) even after 42 days of continuous exposure to wedge prisms (Pick & Hay 1964). While it is *significantly* greater than the effect achieved within a minute or two by staring at a curved line with the naked eye (Gibson 1933 *op. cit.*), it is not very *much* greater. That being the case, one is led to wonder whether there really is adaptation of this kind or, if there is, what factor or factors constrain it from progressively increasing toward full adaptation. To my knowledge, the only plausible hypothesis advanced about this question is that information from eye movement is not altered by wearing prisms in goggles, and it thus continues to support the perception of a curved-image contour as curved. Only prisms that moved with the eyes – or the optical equivalent achieved in some other way – would alter curvature. But now the advocates of this hypothesis have tested it and found it wanting (Miller & Festinger 1977). So it seems to me that this question—i.e. the minute degree of adaptation to altered curvature – ought to be the one to receive priority by investigators in this field.

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Voluntary movement and perception in intrapersonal and extrapersonal space. The very general hypothesis concerning whether neural processing of sensory input is dependent on the organization of motor activity requires further specification before it can be treated theoretically and experimentally. Gyr et al. have judiciously restricted themselves to the experimental testing of a very special hypothesis concerning whether visual perception of straightness with one eye is influenced by voluntary movements in extrapersonal space. Their results seem clear to me: that a 30-min. exposure to extrapersonal space distorted by a prism does not change visual perception of straightness.

The theoretical explanations that sometimes accompany studies of perceptual distortions and illusions, however, make one suspicious as to whether the conceptual framework might not likewise have been distorted! Consider, for example, the classical experiment (Helmholtz 1867) in which displacing one eye (while the other is closed) apparently causes extrapersonal space to move in the opposite direction. To me this statement is meaningless. It is usually assumed that the subject recognizes that extrapersonal space is moving while he is not. But even this statement is inaccurate, because it is not clear what is meant by "the subject is not moving." If the movement is referred to the same reference system, the statement is a contradiction: although extrapersonal space is moving, the subject is not moving with it. If two different reference systems, intrapersonal and extrapersonal space, are introduced, this problem can be solved, but the solution would be a quite special one: The subject is not moving in intrapersonal space, but extrapersonal space is moving. On the other hand, if the subject reaches out and gets hold of a table, this table is not moving relative to intrapersonal space, but the rest of extrapersonal space is moving. By induction, the subject will soon arrive at the conclusion that extrapersonal space is not moving relative to him, and the final answer provided by any sensible subject would be: "Somebody is pulling my eyeball!" The apparent movement disappears; the visuomotor conflict is a conflict in concept definition. In this example it is assumed that proprioceptive and cutaneous receptors inform the subject that he is not moving. This is reasonable, because many proprioceptive receptors can signal steady joint position, and some even signal passive displacement of the eyeball (see Skavienski 1971; and Shebilske on Roland 1978 *op. cit.* pp 161–64). Furthermore, no "corollary discharge," "efference copy" or the like is involved here, because no voluntary movements are attempted by the subject.

If one hopes for an answer to the question as to whether or not voluntary movements can influence the perception of extrapersonal space, the first prerequisite is to specify the reference system in which the voluntary movements are executed. The body is a natural and mobile four-dimensional reference system for voluntary movement [cf. Fraser on Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1 (1) 1978 pp. 22–3]. The eyes, limbs, head, and neck can be moved relative to one another or to the rest of the body. Whatever the voluntary movement in question, the brain is continuously informed concerning the relative positions and positional changes of different body parts by proprioreceptive receptors maintained in calibration in the periphery (see Roland & Ladegaard-Pederson 1977). The bodily reference system is an automatically-updating system. When voluntary movements are to be executed in *intrapersonal space,* the task for the subject is to move a part of the body *relative* to other body parts.

Movements in *extrapersonal space,* in contrast, are movements executed in a three-dimensional reference system fixed by points in the surroundings. The number of extrapersonal reference systems is infinite. Reaching for a teacup on a table is an example of a voluntary movement in extrapersonal space. Unless it is assumed that we are genetically provided with information concerning every conceivable transformation between intrapersonal and extrapersonal space, there is no unique coreference between intrapersonal and extrapersonal space. (The special situation in which the bodily system and the extrapersonal system are under the same influence of gravitional forces requires special treatment, for which there is no space here.) Execution of voluntary movement in intrapersonal and extrapersonal space requires different types of information. To be able to execute a voluntary movement in a particular extrapersonal space, the subject must know the spatial relations as well as transformation between the extrapersonal and intrapersonal space. Extending an arm always involves extension in intrapersonal space, but reaching for a teacup on a table will sometimes consist of arm extensions, sometimes abductions, and sometimes more complicated movements (e.g. when the table moves relative to the subject). Consequently, voluntary movements in intrapersonal and extrapersonal space are always two different tasks for the human brain.

My own cited work (Roland 1978 *op. cit.*) concerned voluntary movement in intrapersonal space in which the thumb and index finger moved relative to each other. It was shown that subjects were aware of both tension and effort, but the explanation provided went no further than to assume that man has a memory for motor commands [cf. Kupfermann & Weiss: "The Command Neuron Concept"

BBS 1 (1) 1978] – in other words, that subjects know what they are going to do when they attempt voluntary movements and are able to remember this. To describe this finding as a central monitoring of one's own motor activity is not wrong, but it is awkward. Voluntary movements must be programmed before they are executed, and this programming takes place in the cerebral cortex outside the primary motor area (Roland et al. 1979a). Any "motor information" *prior* to this planning is nonsense; *during* the planning, it is a tautology; and during the execution, it is simple sensory feedback (see also Evarts 1972). Yet, there has been no physiological evidence of any corollary discharge, re-afferent signals, or efference copy during voluntary movement.

Very recently, however, we have been able to show that the cortical activation pattern in man during voluntary movement is dependent on whether the movements are executed in intrapersonal or extrapersonal space (Roland et al. 1979b). The main difference is that the superior parietal region is activated only during voluntary movement in extrapersonal space. Our technique does not allow us to say whether the activation of these neurons in the superior region is due to signals from the programming premotor regions or is a manifestation of altered neural processing of sensory input, or both. At present, we believe that this finding is best described as consisting of neurons activated in parallel with the other participating cortical areas to provide information both about spatial trajectory in the extrapersonal space in question and the actual transformation between the extrapersonal and intrapersonal (proprioceptive) reference systems for the use of the motor-programming neurons in the premotor area.

In conclusion, there are no "visuomotor conflicts;" the sensory information from an arm pointing toward a target in extrapersonal space bears no relation to the external reference system in question. The relation or transformation function between intrapersonal and extrapersonal space has to be learned in each case, whether we are jet pilots, sailors, astronauts, or subjects provided with wedged prisms.

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Oculomotor hysteresis: implications for testing sensorimotor and ecological optics theories. Oculomotor hysteresis, which is a change in muscle responsiveness after certain eye-movement activities (cf. Collins 1975; Shebilske 1977), can account for many kinds of prism adaptation (cf. Ebenholtz 1974, 1978; Paap & Ebenholtz 1976, 1977) and could be involved in the Held & Rekosh paradigm. It must accordingly be controlled in future investigations within that paradigm. It may also provide a tool for tests of the main issue raised by Gyr et al. – namely: whether motor processes interact with visual processes to produce percepts.

Tests are needed because, although many experiments confirm the dominance of visual information over motor information when the head and body moves or when the environment moves to simulate observer movement (cf. Shebilske 1977), few experiments have investigated the functional significance of visual and motor information in static situations, even though many important percepts, such as the perception of curvature, tilt, and direction, occur when an observer and the environment are relatively stationary. The Gyr et al. pre- and post-tests are relevant to one of these (curvature), which makes their study a welcomed exception, but additional tests are still needed.

The lack of empirical observations has not stood in the way of the generation of theories, especially theories about the perception of direction. In 1950 Gibson speculated that the perception of body parts, including the nose, is an important source of visual information for seeing direction. A recent rendition of this hypothesis was stated by Bower (1974) and tested by Shebilske & Nice (1976), who found it wanting. In 1966 Gibson proposed another hypothesis, based on the fact that the fields of vision for successive fixations have large overlaps, which contains a common structure that could provide the necessary information for directly seeing a constant direction of objects with respect to the self, despite changes in the direction of objects with respect to the direction of gaze. Both of Gibson's hypotheses assume that visual information is sufficient and motor information is irrelevant, which is typical of his more general theory of ecological optics.

An obstacle to the wide acceptance of Gibson's hypotheses about direction has been the observation that people with paralyzed eye muscles see the world move in the direction of intended eye movement, which in turn causes pointing errors (e.g. Stevens et al. 1976); [see also Roland 1978, *BBS* 1 (1)]. Since the pointing errors happen in the presence of visible body parts and structural overlap between fixations, they are contrary to Gibson's hypotheses. This, and the fact that direction is seen accurately without visible body parts or structural overlap, has caused many to hold a sensorimotor theory according to which a critical process in seeing direction is the central registration of the direction of gaze by means of nonvisual information within the oculomotor system (e.g. von Holst & Mitelstaedt 1950; Matin 1976a; Shebilske 1977; Skavenski 1976).

Gibson has not commented on the paralysis studies, but his attitude about similar observations has been clearly expressed (Gibson 1966 *op. cit.*). He considers extreme conditions like paralysis to be inappropriate for testing theories of perception. His argument must be taken seriously, because the most commonly employed perceptual processes could have boundary conditions beyond which qualitatively different processes take over. For example, visual information is used to stabalize eye position in a structured environment, but proprioceptive information takes over in a homogeneous environment (Matin, Matin, & Pearce 1970; Skavenski & Steinman 1970). Similarily, visual information may dominate in the perception of direction, except when it is not available or when extreme motor anomalies exist. Thus, Gibson's argument against the experiments of sensorimotor theorists, along with his failure to provide empirical support for his theories about the perception of direction with the head and body stationary, has created a stalemate.

Hysteresis in the oculomotor system may provide a way to break the deadlock. In a series of experiments still in progress, I have found that hysteresis causes significant pointing errors in a fully-structured visual environment, and that these errors are significantly smaller than those caused by the same amount of hysteresis when the structured visual environment is removed. The first result supports the functional significance of motor information in seeing direction. Unlike past results, it should not be dismissed as being caused by conditions outside the normal operating range of the perceptual system, because hysteresis is within the spectrum of the usual conditions under which the perceptual system must operate in everyday situations (cf. Shebilske 1977). The second result supports the view according functional significance to structured visual information in seeing direction. (In my experiments, extraneous response strategies such as lining up the pointer with the remembered position of a background object were controlled.)

Thus, the results of hysteresis studies add to those of Gyr et al. in calling for a more serious consideration of both the sensorimotor and ecological optics theories of perception. Perceptual systems may be hybrids of the systems suggested by both theories.[1]

NOTE

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Motor system changes are not necessary for changes in perception. Gyr et al. are concerned with the hypothesis "that the neurological processing of sensory input is dependent on the organisation of motor activity," and they translate this hypothesis into operational terms as follows: "It must be shown that with visual input constant, changes in the state of the motor system do produce changes in perception."

These statements refer to a general all-pervasive connection between "all" motor events and "all" perceptual processes. Parsimony in neural interaction, however, would suggest the existence of functional connections between specific motor and perceptual processes. For instance, visual input can signal either subject movement or stimulus movement. If the visual stimulus moving across the retina is the only cue, then it would seem impossible for the organism to make differential interpretation of these two types of movement. However, re-afferent information about eye movement or head movement would provide sufficient information to enable differentiation. The neck and eye muscles are involved in a *particular* efference-afference feedback loop that involves re-afference. If one eye is closed and the other eye is gently tapped, the visual field will appear to jump about. When the eyeball is moved by the finger, the efference copy is irrelevant or has no reference to the eye. The mismatch, consisting of the movement of the eye and the lack of an efferent copy signalling a motor command for the eye to move, endorses the percept as being the visual array that moved.

The specificity of efference-afference feedback loops in perception is often ignored. The above method of moving the eye can be regarded as exafferent

input, simply because the eye movement seems to be independent of any motor command by the organism. Touching the ribs with the fingers in trying to tickle oneself sets up an efferent copy that is relevant to the tactile experience. Re-afference affirms the sensation with the percept of self-initiated touch, and no tickle is perceived. When someone else lightly touches the ribs, there is no efferent copy with the CNS, and the exafferent stimulus is interpreted as tickle.

The above examples illustrate how necessary it is to particularise the relationships between sensory and motor components in perception. A problem with many visuomotor feedback experiments is that they fail to specify those particular motor activities involved in the neurological processing of sensory input that generate specifiable perceptual effects. In a series of experiments Collins has shown that it is essential to specify the relevant muscular stimulation involved in the interpretation of space (Collins 1971; Collins & Lahy 1972; Collins & Lord 1971). Prior to these experiments all sorts of claims concerning motor involvement in judgments of kinesthetic space were being made. Many experimenters (Bakan & Weiler 1963; Moylan 1964; Zacks & Freedman 1963, and many others) used irrelevant muscular stimulation in studying kinesthetic spatial judgments. In much the same way, we feel that it is important to specify the nature of the visuomotor feedback and the processes involved.

The failure to replicate the Held & Rekosh study by Gyr et al. is just another instance of failing to replicate an experiment in this area. In a number of studies (Singer & Day 1966a; 1966b) we have tested Held's active-passive hypothesis relating to prism adaptation and have shown that motor activity is *not* a necessary condition for adaptation to occur. In one of these experiments adaptation was achieved with a perfectly still hand viewed through a wedge prism (Singer & Day 1966c), while S was making verbal judgments of hand position on a scale moved by the experimenter. These data suggest that judgmental activity, but not motor activity, may be a necessary condition for the adaptation process to occur when it is indexed by a motor response.

Gyr et al. recognise that systematic scanning of the visual field may be an important variable in their research. We maintain that this, not walking around in a cylinder, is the most crucial aspect of the experiment – because systematic scanning is likely to introduce judgmental activity. A passive condition – for example, the cylinder moving with S sitting, or someone else moving S about the cylinder—would have helped to sort out the relevance of walking. More specifically, experiments are needed to articulate clearly just what aspects of the motor system interact with visual-sensory processes to produce changes in spatial judgments.

The large literature on adaptation to transformed sensory input makes it clear that the necessary and sufficient condition for adaptation is a discordance between two sources of spatial information. If the change is to occur in a sensory modality and not just to consist of a learned compensatory motor response, then one source of information must be derived via that modality. The other information can come from many different sources, such as from self-produced movement, from the vestibular system and kinesthetic receptors in the neck that signal gravitational information, or from other sensory spatial modalities such as hearing or kinesthesis.

The only form of adaptation that can throw light on Gyr et al.'s question of whether the efferent motor signal is necessary to visual perception is a change in a visual judgment, not a change indexed by any form of motor response. As Gyr et al. note, sensory spatial adaptation of the kind described by Gibson must also be excluded. Of the comparatively few studies concerned with a change in the visual system, some must be excluded, since viewing a laterally-displaced visual field has been reported to produce an oculomotor change in eye position that can also be measured in the post-exposure phase (McLaughlin *et al.* 1966; McLaughlin & Webster 1967). One report of visual change (not confused with oculomotor change) in the absence of any movement comes from Rock (1966 *op. cit.*), who found that 30 minutes of exposure to an optically-reduced image of familiar objects resulted in a significant after-effect no different from that obtained under conditions allowing active manipulation of the objects viewed.

An example of a large change in the visual system that can occur without active motor involvement is the after-effect following exposure to a tilted room (Austin *et al.* 1974). Ss viewed a miniature room tilted 22° and made 10 judgments of the verticality of a bar at the back of the room (but without receiving kinesthetic stimulation from it); they showed a visual after-effect of 4.05° when tested 15 minutes after the exposure period ended. This procedure clearly precludes Gibson's sensory spatial adaptation.

Finally, the suggestion that motor activity has a critical role in visual perception is an extreme interpretation of the sensorimotor theory and one that the Gyr et al. replication does not test. It is also inconsistent with our present knowledge of nervous system functioning. With respect to the question broached by Held & Rekosh as to whether "the subjective geometry of the visual field can be altered by movement-dependent feedback" (1963 *op. cit.* p. 722), the examples given above should suffice to show that there is evidence that, while centrally-monitored motor output may be a sufficient condition for a change in the perceptual process, it is not a necessary one.

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Methodological considerations in replicating Held and Rekosh's perceptual adaptation study. Perhaps the Gyr et al. failure to replicate the H & R result could be due to small differences in method. I would be reluctant to dismiss the H & R finding because of this negative result, especially since one very thorough study has found curvature adaptation beyond that attributable to normalization (Cohen 1965).

Gyr et al. hint at, but do not spell out, what may, I think, be a crucial difference. H & R do not specify the texture density of their "random" field. They also fail to specify the visual angle of the bars in their test grating (Gyr et al. also omit this). We now suspect that the visual system processes not the specific features in a given scene, but rather the spatial frequency content (see Campbell 1974, for a summary). If the visual system is doing a Fourier analysis on input, then common spatial-frequency components between exposure and test conditions may be necessary for the curvature after-effect to be demonstrated. Thus, H & R may have fortuitously hit upon a "random" pattern whose fundamental Fourier components were similar to those of their test grating. Gyr et al.'s exposure and test-stimuli's spatial-frequency components may have been too widely separated for an effect to be generated. (For examples of perceptual after-effects dependent upon spatial frequency, see Anstis 1974, or Ware & Mitchell 1974.)

One additional point: Walking involves some vertical displacement. In the H & R passive condition Ss were wheeled about in a cart. The active condition therefore involved some vertical displacement as well as horizontal translation, and this could provide additional information leading to active-passive differences.

The appropriate experiment remains undone. The basic H & R experiment should be repeated with: 1) movement in the active and passive conditions restricted to pure translation of the head toward the random field, and 2) test and exposure fields having equivalent spatial-frequency content.

NOTE

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The thesis of the efference-mediation of vision cannot be rationalized. I wish to argue that there is neither an evolutionary nor a logical reason for an efference-mediated mechanism of visual perception. If this argument is valid, it follows that any experiment intended to evaluate such a mechanism is evaluating something quite different, and that both classical and contemporary data gathered in reference to the efference-mediation issue will require careful re-examination and re-interpretation.

Optical flow perspective and physical facts at the scale of ecology. Let me identify at the outset a physical fact at the scale of ecology that, by any reasonable account, has held true for the entire course of evolution: When an animal locomotes, its body moves as a unit relative to the surroundings, but the surroundings (say, for a terrestrial animal, the ground plane and the objects that clutter it) never move as a unit relative to the animal. (Earthquakes might appear to be an exception. We could easily rule them out of contention on grounds that their occurrence is too uncommon to pressure the evolution of perceptual mechanisms. But it is more important to note, given the argument that follows, that earthquakes will not structure the light in ways identical to the ways light is structured when an animal moves relative to its surroundings.)

Here is a rough description of the light to the eyes of animals as they move about in their cluttered habitats. The surfaces comprising habitats are opaque and textured. A texture element is tentatively defined as a surface region bounded by a closed curve so that no intensity transitions exist within the region but a discontinuity in intensity does exist at the boundary. For any point of observation in an animal's habitat, the light reflected to that point from the variously-articulating opaque surfaces may be construed as a set of polar projections from the (unoccluded) surface-texture elements onto a projection surface. The polar

projections from a natural surface-texture element onto a mathematically-convenient projection surface can be referred to as an optical-texture element; and the set of those optical-texture elements can be referred to as the optic array (Gibson 1961; 1966 *op. cit.*; Lee 1974; 1976).

When an animal – be it terrestrial, aquatic, or aerial – moves relative to its surroundings, the optic array will undergo a concurrent transformation in all its parts. Thus, if an animal advances rectilinearly in any transparent medium (air, water), there will be an outflow of optical texture (with the center of the outflow specific to the direction of locomotion); if an animal drops from a higher to a lower ledge, there will be a concurrent upflow in all optical-texture elements, and so on. The point to be doubly underscored is this: A global transformation of the optic array is specific to a movement of an observation point relative to the surroundings. This specificity holds for any contemporary animal locomoting in its natural habitat, and it has held, by all reasonable accounts, for any present-day animal's ancestors. Importantly, no *sensible* case can be made for the claim that global transformations of the optic array specify for an animal a unitary movement of the surroundings relative to the animal. For the latter claim would be tantamount to saying that it has been common-place during evolution for the planet earth to move relative to the animals that inhabit it. In contrast, a sensible case can be made for the claim that transformations of parts of the total optic array relative to the total optic array are specific to changes in parts of an animal's surroundings relative to the animal.

No evolutionary motivation for efference compensation. There is therefore no substance to the often-voiced assertion that movement of the animal and movement of the surroundings are signalled by identical stimulation. On the contrary, the two kinds of movement are specified in the circumstances in which animals live and with respect to which they have evolved by very different patterns of visual stimulation. And we see, in short, that there is no evolutionary motivation whatsoever for "mechanisms that compensate for" the visual stimulation produced by movements of the perceiver relative to the surroundings. To be terribly redundant, these efference-mediated mechanisms have been promoted over the years on the assumption that self-movement and environment movement have the same visual consequences, and that an animal therefore needs some special, extravisual mechanism to distinguish its movements from those of its surroundings. But since the optical consequences are not identical and never have been, in the lengthy past of evolution, we should not suppose that nature was pressured into engineering the special brain mechanisms advocated.

The significance of the above line of reasoning—that there is no evolutionary rationale for the mechanism proposed by von Holst (1954 *op. cit.*) and by Sperry (1950 *op. cit.*) – seems to have escaped Gyr and his colleagues. They try to disarm the argument of Gibson (1966 *op. cit.*), that is under elaboration in this commentary, by the feeble conjecture that while global visual transformations may not be equivocal for a fly, they could be equivocal for a human. The conjecture is curious on two counts. First, Gyr et al. offer no logical or evolutionary reason why humans should be special in this regard. The facts of optical flow perspective are commensurate with the facts of physics at the scale of ecology – why should humans compromise them? Second, there is already substantial evidence in the literature contrary to the conjecture. Thus Lee and his co-workers (Lee & Aaronson 1974; Lee & Lishman 1975; Lishman & Lee 1973) have demonstrated repeatedly that in a room whose floor is stationary but whose ceiling and walls can be made to move as a unit, humans perceive themselves to be moving relative to the room when the room is moving relative to them. Moreover, when the room moves rectilinearly with the person, at the same velocity and in the same direction (that is, no global optical outflow accompanies the act of walking forward), the perception tends to be that of not moving relative to the surroundings, although the parts of the body are perceived as moving relative to each other in the manner of walking.

Efference is equivocal. The latter observation coupled with a more simple phenomenon – that of walking on a treadmill – brings home a fact of some considerable importance for the von Holst (1954 *op. cit.*) model and for efference-based models of perception in general. Recall that the raison d'être for von Holst's model is that afferent signals are equivocal on the issue of whether the animal moves relative to the surroundings or the surroundings move relative to the animal; therefore, one appeals to efference to resolve the equivocality. But efference, it can be argued, is itself equivocal; in the case of walking forward in Lee's moving room or on a treadmill, the efference is the same whether or not one is displacing as a whole relative to the surroundings. Presumably, then, advocates of efference-mediated visual perception should propose an additional mechanism, one that appeals to afference – more properly, optical-flow perspective – to resolve the *efferent* equivocality so as to determine whether or not forward locomotion is taking place!

We ought to note that the treadmill case is not especially exotic. For the bird or insect flying into a wind, the fish swimming upstream, and the primate pushing or pulling a relatively immovable object, patterns of efference in these natural circumstances can be said to equivocate on movement relative to the surroundings, whereas optical flow perspective would be singularly univocal. In sum, the ambient optic array is expropriospecific (Lee 1978); efference is not.

Visual information for the control of activity rather than response-eliciting stimuli. The arguments above and elsewhere (Turvey 1977a) underscore the absence of sensible reasons for efference-mediation of visual perception. Let us accordingly take another look at the experiments directed at demonstrating its existence.

It is assumed in the experiments of von Holst & Mittelstaedt (1950 *op. cit.*) that a striped drum rotating about an insect triggers a reflex, the optokinetic reflex, that rotates the animal in a direction opposite to that of the rotating stripes. The "stimulus" for the reflex is said to be a difference between the angular velocities of the stripes and the animal. But Varju (1975) has shown that when the insect is allowed to move freely and make normal scanning movements, the insect rotates *with* the rotating stripes at a constant rate rather than lagging behind at some value correlated with detection of slippage. Indeed, an insect rotating with the stripes, and taking one of them as a piece of the surround to keep aligned with, may – if it finds itself falling behind the fixated stripe – make a fast turn backwards *against* the direction of rotation and alter its fixation to a following stripe. On other occasions the insect may make a jump that takes it *ahead* of the rotating stripes. These observations suggest that rotation of the visual array relative to the animal is not a stimulus triggering a response but information about the fact that the animal is being rotated relative to its surroundings, and that the animal behaves in *varied* ways to preserve a fixed relation to its surroundings.

Consider another example. Srinivasan and Bernard (1977) superimposed a pursuable object on a large moving pattern. Normally, for a fly tethered in front of the pattern in such a way as to permit it to fly, the moving pattern would be responded to by wing-amplitude adjustments that right the insect with regard to the coordinates of the surroundings. In the presence of a pursuable object, however, the fly selectively ignores the large moving pattern that normally elicits a classical type of optomotor response until the pursuable object disappears [cf. *Henn, Vonèche*].

"Rules" for controlling locomotion. There are two points to be made: First, that the optical flow perspective, jointly specifying the surroundings and the self, is information for the control of behavior; and second, that the role that information plays depends on the control "principle" or "rule" in operation at the time. Consider the following as examples of the "rules" for *visually*-controlling locomotion: In order to hold one's position relative to the surroundings, move so as to cancel any global optical transformation; to turn the body toward an object, move so as to produce a rotational optical flow away from the location of the object; to approach an object, move so as to make the optic array flow outwards, with the object at the center of the outflow.

My strong preference is against construing these as rules or commands, invested in the brain or issued from the brain (see Fitch & Turvey 1978; Gibson, in press; and Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1 (1) 1978); rather, they are *laws of physics at the scale of ecology.* Writing them in sentence form encourages the idea that they are rules to be enforced by an enforcer; but this self-actional interpretation is at best regressive and at worst implies sui generis control (see Bentley 1954; Dewey & Bentley 1949; Shaw & Turvey, in press). What is needed is an interpretation that is considerably more consonant with the scientific enterprise and considerably tougher to come by – namely, that the control "rule" arises within the animal-environment system as a consequence of the mutual constraints of an animal and its environment. I make this remark here because Gyr et al. comment on the "complexity" of the efference-mediated view of perception versus the "simplicity" of the direct-realism view advocated by Gibson and others (such as myself). If, by a complex theory of perception, they mean that it prescribes very involved mental gymnastics to achieve perception, then the contrast is fair. But if by complex they mean the kinds of concepts *required by science* to account for perception and the control of activity without fall-back concepts that intimate unanalyzable internal interpreters, ascribers of meaning, and initiating powers, then I must take issue. The program of a committed (direct) realism is conceptually far more demanding (Shaw & Turvey, in press; Shaw, Turvey, & Mace, in press). And, on the subject of demandingness, it is not relatively easy, as Gyr et al. claim, to observe and

control the variables of vision – not when one is describing light at the scale of ecology in reference to the activity of animals (Lee 1974, 1976) and the perception of environmental events (Shaw & Pittenger 1977).

The fly of von Holst and Mittelstadt. Returning to the fly in the optomotor drum, when the drum is rotated about the fly and the extant control rule is to stay put, the optical flow specifies that the fly is turning relative to its surroundings, and it accordingly trys to rectify matters. When the extant rule is to turn to an object, the optical flow specifies that the animal is turning relative to its surroundings and in the right direction. Thus it keeps turning until aligned with the object.

Now consider the case where the fly's head is rotated 180°. The consequence of rotating the fly's eye would be interpreted by some as consonant with conventional physical optics and the idea of a retinal image, and contrary to the ecological optics promoted in this commentary. This is not the place to repeat the arguments against the retinal-image concept. Those arguments have been given in considerable detail (Bentley 1954; Gibson 1966 *op. cit.*; Turvey 1977), and they are sufficiently strong on independent and broadly-based grounds to suggest that the consequence of rotating the head (or the eyes) is only an apparent anomaly for the ecological-optics perspective. For the present it suffices to point out that a resolution of the anomaly must begin with the fact that the optical structure that the fly's visual system uses is not symmetric under the head-rotation transform (Mace, personal communication). At all events, given that the optical flow perspective under the 180° head-transformation specifies movement *away* from the object, and that the extant control principle is for turning *toward* the object, the fly engages in behavior to oppose the turning away.

On reinterpreting the passive versus active data. Vision is capable of obtaining three kinds of information (Lee 1978): exterospecific information about the layout of surfaces (objects, events), propriospecific information about the layout of parts of the body relative to each other, and expropriospecific information about the body and body parts relative to the layout of surfaces. These three kinds of information hold for vision with prismatic distortion just as they do for normal vision. And the claim is easily ventured that different experimental manipulations (see Kornheiser's review 1976) impinge differently on these three kinds of information. The following also holds for distorted and normal vision: Variation in optical structure reveals nonvariation and permits the distinguishing of styles of change from nonchange. It follows, therefore, that the richer and more varied the natural transformations of optical structure that the observer-wearing-prisms experiences, the greater the opportunity to distinguish the novel transformational invariants specifying styles of change (e.g. observer relative to surroundings, limbs relative to body, objects relative to surroundings and relative to observer) from the novel structural invariants specifying the structures participating in the changes (see Pittenger & Shaw 1975; Turvey 1977). On such an ecological-optics analysis, active-passive is not the dimension of significance for the study of adaptation (cf. Kornheiser 1976). Rather, the concern should be a rigorous (mathematical, experimental) analysis of the various transformations (including the null case) of optical structure arising from movements of the animal or changes in the surroundings and the kinds of information those transformations make available. The latter concern, and that for understanding control rules and how they arise, define well-motivated scientific problems. The proposal for the mediation of vision by efference does not define a well-motivated scientific problem; in my view it is a proposal without any "residual plausibility" (in the words of Gyr et al.) whatsoever.

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Visuomotor feedback: A short supplement to Gyr's journey around a polka-dotted cylinder. My intention is to write a short supplement to Gyr et al.'s study, dealing with two of the points in the paper: 1) the theoretical question as to the necessity of observer movement for perceiving the properties of an object, and 2) the empirical findings under dicussion. I shall propose the embryo of an experiment to test visuomotor feedback in animals and humans.

It seems to me that the French mathematician Henri Poincaré has shown once and for all the *logical* necessity of movement for the existence of object properties such as shape, size, and permanence in space. Without his "group of displacements," such invariants could not be established, and we would all be in the position of Sperry's frog trying to catch our daily flies in the wrong quadrant of the trigonometric circle. There is an American phrase that expresses the same thing more forcefully by alluding to a hole in the ground to be distinguished from another one located on the observer, but *BBS* is too academic a journal to print anything about academy figures.

Gyr et al.'s subjects seem to demonstrate that such a distinction is not clearly made by human beings under certain conditions, so I would like to submit two pieces of experimental evidence that I have collected that could help us understand Gyr et al.'s results, especially since nonadaptation could be explained in a variety of ways.

In an unpublished experiment run for the Geneva Astronomical Observatory on the question of the existence of star rings in the sky, I showed that astronomers could detect "rings" in a computer-simulated series of "star photographs," in which the location of the various stars was randomly distributed on the photographic surface presented to the Ss (who were *not* Geneva Observatory astronomers). But – and this is the relevant piece of data – the distribution of ring-detectors in the sample of Ss was not significantly different from chance level. This result persuaded us to follow up this point with a larger sample of "naive" Ss (astronomers are not so numerous, and they are very busy), who had to observe random arrays of colored dots of the sort described by Gyr et al. in their experiment. The same results were obtained, with the following additional effect: Ss would find "lines" and "rings" significantly more readily when instructed to "look for regular configurations" or just "regularities."

This last result could indicate that H & R instructed their own subjects in such a way as to induce a certain type of response instead of another, since the organization of randomness into order seems to depend so evidently on directed attention.

The second piece of evidence is briefly mentioned in my book on figural after-effects (Vonèche 1971). In an experiment conducted with David Bearison to separate the Gibson effect from adaptation, we presented a curved line of dots to children (aged 5 to 12 years) wearing prismatic lenses that made the line appear vertical. We expected this procedure to rule out what Gibson calls the "normalization" effect. The results were surprising: the younger children did not show any adaptation, while the older ones displayed adaptation only to the upper part of the "line."

This result tends to show that dotted lines are not perceptually equivalent to continuous ones; hence, when put together randomly, they require highly-trained observers to be perceived as lines, especially since the sequence of dots chosen as "line" dissolves as a function of head movement.

What, then, could be a good test of visuo-motor feedback? It seems to me that it should consist of a procedure allowing for a clear distinction between the optomotor reflex and compensatory movement. The following condition could be critical for this: instead of having just one stationary cylinder, as in H & R's and Gyr et al.'s experiments, I would propose having two concentric cylinders of almost the same diameter (just enough to allow for rotation without friction) of which one, the inner one, would be stationary and half as high as the other, which would be rotating at a constant speed. Both cylinders would be painted with alternating white and black vertical stripes. S would be brought inside the apparatus blindfolded. Once the cylinder was rotating, the blindfold would be removed and S's responses observed. Visually, it is impossible for an observer to distinguish between real and apparent movement inside the cylinders, since the two cylinders seem to move in opposite directions, as far as the mere succession of retinal images is concerned. On the basis of Wapner and Werner's (1957) sensory-tonic theory, my expectation would be that lower animals (and probably brain-injured patients) would exhibit ipsiversive visual tracking of the rotating cylinder, followed by active pursuit of it, whereas normal human adults would track with compensatory movements in the opposite direction. In addition to verbal (when possible) and motor responses, a double check could be provided by separate optometric measurement of S's vestibular, optokinetic, and post-rotatory nystagmus [cf. *Henn*].

This is only a thought experiment, and things are certainly more involved than this test. The only aim of this contribution is to lay the groundwork for spelling out the necessary and sufficient specifications for a good, crucial experiment of the central problem tackled by Gyr and his collaborators.

***by* Richard D. Walk**

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Attentional factors in depth perception. The H & R study is, in my opinion, an excellent one. That they both predicted and obtained adaptation in the random-texture condition was not surprising to me; the experiment was an extremely ingenious demonstration of their own position. What of the Gyr et al. replication?

The studies seem dissimilar enough so that I, for one, would prefer to suspend judgment until others have tried to replicate the study. If the replications fail, and if they do not shed any light on the conditions under which the H & R results appear or do not appear, then we should consider the theoretical implications.

My own position is in disagreement with Held's, in that I feel that some of the developmental phenomena that he feels are acquired through interaction with the environment are unlearned. To this end, in a modified replication of Held & Bauer (1967) we tested monkeys reared without sight of the hands and found little deficit in visual reaching (Walk & Bond 1971). We also reared kittens for a short time in the dark – shorter than did Held & Hein (1963 *op. cit.*) – and found evidence for depth discrimination when the passive and dark-reared kittens were tested (Miller & Walk 1975). Held & Hein (1963 *op. cit.*) had found depth discrimination for active, not passive, kittens. But, except for their position on the early development of visual-motor behavior, I am basically neutral as to the role of re-afference in behavior.

Three experiments that we have performed with kittens (and are still carrying out) are relevant to this issue. The first experiment, referred to above (Miller & Walk, 1975), involved raising kittens under four conditions: 1) normal rearing in the light; 2) dark rearing for 17 days and then active locomotion for 3 hours a day for 10 days; 3) as in Group 2, except the kittens were passive, confined to a holder, able to see the environment, but unable to see their limbs; 4) in the dark until tested at 27 days of age. We found active animals to be similar to passive ones except for the first visual-cliff test. All groups discriminated shallow from deep sides of the visual cliff on a "calling test" in which they were called by the experimenter to come to him.

We next had a closer approximation to the Held & Hein (1963 *op. cit.*) study with the same four groups. The deprived animals remained in the dark for 56 days, then Groups 2 and 3 had ten days of visual exposure, and all groups were tested on the 66th day. These results were almost exactly like those of Held and Hein. The active group was excellent, as was the normally-reared group, while the passively-exposed and the dark-reared kittens were poor on depth descrimination on the visual cliff and when called by the experimenter from the shallow and deep sides.

These results led us to pick a middle period to test for the effects of increased attention on depth discrimination (Walk, Shepherd, & Miller 1978). We had the same four groups and added two "attention" conditions for the passive animals. Kittens were raised in the dark for 40 days before the active and passive groups were given 3 hours a day of visual exposure. The attention groups were, first, a group that watched a visual display and, second, a group that could control forward locomotion. The first, attentional (or "car-watching") group remained in their holders while they watched a toy roller-coaster with small cars that continually circled a track. The other attention group was a passive locomotion (or "go-cart") group; these kittens remained in their holders, but they could lift their heads to close a microswitch that controlled forward motion in a circular path. One animal made as many as 300 revolutions in the 3-hour period.

Our results are preliminary, but the two passive-attention groups seem roughly similar and not different from the active group, while the poorest groups are the regular passive kittens and the dark-reared ones. We hope that additional kittens will continue the same trend.

What might this mean? It would mean that "attention" can maintain depth perception that would be lost without it. The regular passive animals in holders typically seem to close their eyes for long periods; with nothing interesting in the environment they shut it out. Many experiments on prismatic adaptation have appealed to attention as a factor in perceptual-motor adaptation (Kornheiser 1976). Is attention, then, an alternative to self-induced locomotion? Is self-induced locomotion no more than a method for maximizing the attention of the animal? It would be premature to conclude this, even if our results continue to be the same after further testing. In our enthusiasm we had three animals that went 56 days in the dark before receiving additional attentional exposure. These animals were impaired and more similar to passive animals than to active-locomotion animals.

Suppose all of these results hold up? I would then hypothesize that depth discrimination is unlearned, that attentional factors can maintain it for some time, but that self-induced locomotion is needed for its efficient maintenance or recovery after prolonged periods of deprivation. Is this "re-afference" in the Held sense? I do not know, but the re-afference of self-induced locomotion is indeed powerful for recovering or maintaining depth perception.

Despite my disagreement with some interpretations of the Held research, I am indebted to him, as is psychology, in many ways. First, the experiments produced by him and his associates are ingenious, creative, and productive. The best-known research ranges from the prismatic adaptation research with adults to its thematic extension with orphanage children, kittens, and monkeys. Recently, he has produced distinguished research on the visual acuity of young infants with many practical implications. Second, the theory has been productive in terms of the research produced by him as well as by others. A strong theory inspires both refutation and extension, and psychology is the richer because the interaction of theory and experiment has helped us to understand visual-motor behavior. Indefinite theories spark little research. It takes a strong person to stick his neck out, and I feel perception and psychology have been enriched, and will continue to be enriched, both by Held's theory and by his experiments.

***by* Hans Wallach**

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Three functions of motor-sensory feedback in object perception. What is the function of motor-sensory feedback in visual and auditory perception? I shall try to answer this question by discussing three kinds of object perception where motor-sensory feedback is essential.

1. *Processes that bring about the perception of a stable environment.* When we move we produce relative displacements between the environment and our eyes or ears, leading to visual or auditory stimulation that, taken by itself, is indistinguishable from stimulation that might be provided by some objective motion. Such stimulation would, therefore, cause perception of environmental motion were it not accompanied by motor-sensory information representing the body movements that caused the relative displacements. A compensation takes place in which the visual or auditory information about motion is more or less accurately matched up with motor-sensory information, leading to nonperception of movement-produced displacements. We now know of five movement-produced sensory inputs for which such compensation occurs. They are: image displacements due to eye movements (Mack 1970; Mack & Herman 1978); changes in visual direction due to head-turning or nodding (Stratton 1897; Wallach & Kravitz 1965a; Wallach & Bacon 1977); changes in auditory direction due to head-turning (Wallach & Kravitz 1968 in Wallach 1976); rotation of the visual field due to head tilting (Wallach & Bacon, 1976); and rotation of objects one passes when moving forward (Wallach et al. 1974 in Wallach 1976). The accuracy of these compensations has been measured by a method designed by Wallach & Kravitz (1965a). The method consists in adding objective motion that is physically dependent on the subject's movements to the relative motion caused directly by the subject's movements. The proportion of added objective motion needed to cause perception of that objective motion measures the accuracy of the compensation – the precision with which the visual (or auditory) input and the motor-sensory information are being matched up. This proportion was found to vary widely. It is about 20% for eye movements, 3% for head-turning and visual direction, 15% for head-turning and auditory direction, 5% for head-tilting, and about 40% for rotation caused by moving forward.

The variety of these compensatory processes is actually quite limited – namely, to subject-relative displacements – as the following case shows. When one turns one's head, the amount of displacement of a stationary object relative to the eyes also varies with its distance from the eyes. This effect of distance is taken into account in the compensation process as well (Wallach et al. 1972 in Wallach 1976). Of two objects at different distances from the eyes, each one will be seen as stationary during head-turning when it is given singly. But when they are simultaneously visible, one object will be seen to move. Then they are also displaced relative to one another, and this object-relative displacement amounts to a change in configuration. Although the object-relative displacement is caused by one's own movements, there is no compensation; one of the objects is seen to move. While there is compensation for the movement-produced displacement of each object, there is none for the emergent configuration change. This is a striking instance where motor-sensory feedback cannot touch figural perception. It fails to have an effect on the configurational process, although it affects its parts.

2. *Perceptual processes where movements have an information-gathering function.* In order to interest us here, such a process must have two characteristics: that movements elicit sensory inputs unavailable without them, and that motor-sensory information about the movements be needed in the processing of these inputs. I know of only one instance where the second characteristic is certain – namely, auditory localization. Perceived sound directions vary in two spatial dimensions. One dimension, the angles that the sound direction forms with the aural axis, is mediated by time-of-arrival differences at the ears. Information about the other dimension, the angle that the sound direction forms with the horizontal plane, is obtained by head movements. This angle of elevation is given as a quotient between the changing angle representing the time-of-arrival

difference and the changing angle representing the head rotation (Wallach 1940 in Wallach 1976). Elevated perceived sound directions can be produced by displacing a sound source in the horizontal plane dependent on the head-turning. If, with the displacement of the sound source constant, the head rotation is made larger or smaller, the elevation of the sound direction becomes smaller or larger.

I do not believe that it is possible to conclude from this particular case, and others like it which may yet be found, that motor-sensory feedback plays a pervasive role in object perception. Such cases fill specific gaps where stimulation of the pertinent modality alone cannot provide needed information.

3. *Adaptation in visual perception of shape that requires movements on the part of the subject.* In addition to the displacement of the visual direction, wedge prisms cause two major shape distortions: straight lines parallel to the base of the prism become curved, and there is a distortion of distances in the apex-base dimension, in which distances near the apex are lengthened and distances near the base are shortened. As long as the observer remains motionless, these distortions could be properties of the visual environment. Only when the observer moves in such a way that the shape distortions shift relative to the visual environment and cause deformations in the pattern reaching the eyes are the distortions revealed as matters of the viewing conditions.

Wallach & Flaherty (1976) obtained rapid adaptation such that the distance distortions caused by a wedge prism became diminished. During the exposure period Ss wearing base-up or base-down prisms made nodding head movements while looking at a regular pattern of horizontal stripes. After exposure the regular pattern looked distorted, and this effect was measured by compensation. During exposure the nodding head movements caused the prism to tilt up and down, and this tilting transformed the distance distortion caused by the prism into deformations.

It seemed possible that head movements were needed here only to transform the shape distortions into deformations; in that case motor-sensory feedback would have no role in this adaptation. Wallach & Flaherty, however, showed that this is not so. In a variation of their experiment, head-nodding was replaced by having the prism, no longer fixed to S's head, tilt on its own. Although this arrangement caused the same deformations to reach S's eye that were caused by nodding, the adaptative alterations failed to develop. Motor-sensory feedback did play a role in this adaptation.

A corresponding result was obtained by Wallach & Barton (1975), who changed the curvature effect of the prisms into a depth effect, which was much more conspicuous then the curvature. They used the curvature effect to produce retinal disparities, which, in turn, caused a strong concavity to be perceived in patterns located in S's frontal plane. Again, only deformations produced by S's nodding head movements caused adaptation; deformations produced by shifting the pattern relative to the distortion, with S's head stationary, did not. Here, then, are two instances where motor-sensory feedback is essential for shape adaptation.

The experiment by Gyr et al., in which the walking subject was a dot pattern shift through the prism worn base-up, corresponds in most essential features to the successful experiment by Wallach & Flaherty. Gyr et al. probably did not obtain an adaptation because the deformations caused by the curvature distortion were too small. No deformation connected with the curvature effect would occur under the conditions used by Held & Rekosh – that is, from a horizontal displacement between the head and the environment when the prism is worn base-right. I agree with Gyr et al. that no adaptation can be expected to develop under these conditions.

Do the experiments of Wallach & Flaherty and of Wallach & Barton demonstrate that motor-sensory inputs play a role in shape perception as such? I think not. To be sure, their results show that deformation by itself is not sufficient to cause adaptation, and that the deformations must be accompanied by head movements. But the motor-sensory feedback from these movements has no direct bearing on the shape distortions that are eventually altered by adaptation. The feedback is covariant with the deformations, and this covariance apparently initiates the adaptation process. There are no grounds for believing that the feedback has a direct effect on shape perception.

To sum up: motor-sensory feedback has several functions in object perception, but there is no evidence that it directly affects the perception of shape and configuration.

***by* Robert B. Welch**

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Separating the issues involved in the role of bodily movement in perception and perceptual-motor coordination. Gyr et al. have used Held & Rekosh's (1963 *op. cit.*) comparison of active and passive movement in adaptation to prismatically-induced curvature, and the current attempt to replicate this experiment, as the context in which to raise three important theoretical questions: a) Can non-optic factors influence or determine visual perception? b) To what extent is motor activity involved in the neonatal development of perception? and c) Is motor activity a necessary condition for visual adaptation to prismatic distortion in adult subjects? Although related, these questions must be addressed separately. This is particularly important here because, as will be seen, it is only the last of these to which H & R's experiment and the present attempted replication are directly relevant.

Non-optic factors in visual perception. As Gyr et al. note, the fact that movement of the visual image across the retina is experienced quite differently if this motion is the the result of active head or eye movement than if it is due to physical motion of the environment, would appear to provide an affirmative answer to the first question. The authors argue that in order to refute Gibson's claim that visual experience can be completely understood in terms of the optic array (the "direct" theory of visual perception), it must be demonstrated that it is the *central* (efferent) component of the motor activity that is crucial in the maintenance of visual stability during bodily movement. This may be an unnecessary requirement, however, since even the demonstration that proprioceptive, vestibular, or other nonvisual inputs can serve this purpose would represent negative evidence for Gibson's theory. Indeed, very recent evidence suggests that neural feedback (afference) may be used to maintain visual stability during active eye movements (Shebilske 1977), contrary to the long-held belief that the extraocular muscles are incapable of signaling eye position.

In any event, it is incorrect to use the results of H & R's study as support for the conclusion that *concurrent* nonoptic factors can affect visual perception. That is, even if it were shown that active bodily movements are necessary for visual adaptation to prismatic curvature, and that the central component is crucial for this process, it would not therefore have been demonstrated that under these circumstances visual perception has a motor component. Gibson (or others) might merely claim that as a result of active motor involvement the observer comes to detect new things about the visual array which result in adaptation. Thus, it is important to distinguish between motor activity as a neccessary *pre-condition* for subsequent visual change and motor activity as a necessary *concomitant* of a unique visual experience. Presumably, only the latter constraint would represent a blow to Gibson's theory.

Motor activity and perceptual development. Studies of adult adaptation to prismatic distortion do not directly illuminate the issue of perceptual development. As Held and his colleagues acknowledged at the very outset of their brilliant series of studies on prism adaptation, the presence of perceptual plasticity in the adult organism is no guarantee that the perceptual capacity in question was originally acquired from experience, or that it was acquired in the same fashion as adaptation in the mature, experienced organism. In short, it is invalid to generalize from adult re-arrangement studies to perceptual development in the neonate. To properly evaluate this question one must examine neonatal organisms, as Held, Hein, and their associates (e.g. Held & Hein 1963 *op. cit.*; Hein, Held, & Gower 1970) have done. Unfortunately, the initially promising results of these studies have been subjected to serious criticism and re-interpretation (e.g. Ganz 1975).

Motor involvement in prism adaptation. Finally, we come to the issue of whether active (versus passive) bodily motion is necessary to produce (partial) adaptation to prismatically-induced curvature in adult observers. Although H & R found support for their prediction that active movement is a necessary condition for curvature adaptation, it has never been apparent how their "re-afference theory" actually applies to visual perception – a mystery that Gyr et al. have not attempted to resolve. Furthermore, it has been demonstrated by Victor (1968 *op. cit.*) that curvature adaptation can be effected by *passive* movement, given certain types of input (e.g., that resulting when the observer moves parallel to prismatically-curved lines). The latter fact suggests that it is not the presence or absence of active bodily movement that is crucial for the occurrence of adaptation, but the availability of unambiguous *information* about the nature of the prismatic distortion. Under some circumstances, as for example the random-dot environment of Held & Rekosh and the present experiment, active movement may provide particularly good information about the distortion. Furthermore, as Gyr et al., along with Victor (1968 *op. cit.*) and Rock (1966 *op. cit.*), have observed, an especially informative combination of bodily movement and visual feedback is provided by locomotion with base-up or base-down prisms.

Parenthetically, it is important to note that the relevant movements are of the entire body or head, but *not* the eyes (as Gyr et al. inadvertently suggest by their use of the term "scanning"). Clearly, unless the prisms are attached to contact

lenses, eye movements will in no way inform the subject that anything is wrong with his vision. This is not to be confused with the point that Gyr et al. raise about the importance of fixating a given spot while walking within the cylinder, a procedure which, although probably not *necessary* for adaptation, might facilitate it.

It is unclear from a comparison of the two studies why it is that Gyr et al. were unable to replicate the H & R results. Unfortunately, their criticism of the latter investigators for failing to use the optimal situation for curvature adaptation is greatly weakened by their own inability to find any adaptation with either this or the "traditional" prism-base orientation.

Clearly, there is a need for further research aimed at delineating the conditions under which adaptation to prismatic curvature will occur. It is conceivable that the advantage of avoiding the Gibson effect by eliminating all straight lines in the visual field is more than offset by the potential disadvantage of not providing the salient information about the nature of the distortion that arises when straight lines are present. Since a few minutes of stationary prism exposure to these lines prior to the adaptation period will produce all of the Gibson effect that will ever occur, pre-exposure measures taken at that time should be free of this effect, and therefore any pre/post shift in apparent curvature should represent an unambiguous measure of "genuine" curvature adaptation.

Authors' Response

by **John Gyr, Richmond Willey,** *and* **Adele Henry**

Motor factors in perception

The points of view represented in the commentaries on our attempted replication of the H & R study on motor-sensory feedback and the geometry of visual space fall into three broad categories. There are commentaries that are broadly theoretical (1) and those that are more narrowly focused on the possible reasons why the replication, or experiments on adaptation in general, might produce negative results (2). The former can be further subdivided in terms of those that are supportive of the theoretical position one can ascribe to Held and his coworkers on these matters (1.1) and others that, for a large variety of reasons, are critical of such a position (1.2). All these points, together with still finer subdivisions, will be taken up below.

1. Comments pertaining to the general theory of motor-sensory feedback in visual perception

1.1 Comments supportive of Held's theoretical position: 1.11. Support from logical considerations. Vonèche reminds us that the eminent French mathematician Henri Poincaré (1952, 1958) concluded by logical argument that the delineation of object properties like shape, size, and permanence, presupposes observers who can move around and who know when they have moved. Only under these circumstances, according to Poincaré, can the distinction between changes of position and changes of state (e.g. changes in color) be made. The former are changes that an organism can bring about by its own movements, or for which it can compensate. Starting from this premise, Poincaré brings principles of mathematical group theory to bear on the formalization of the various possible changes of position. This is the same group theory to which Gibson (1966 *op. cit.*) alludes, without perhaps taking into account that his notions of how the organism obtains information about its own movements does not, logically, comprise the whole set of "knowing that one has moved." From a purely logical point of view, at least, such a set might well include efferent information. Our Response will consider whether, in addition to the logical argument, there are psychological and neurophysiological reasons for expanding the set proposed by the theorists of direct visual perception.

1.12. Supportive comments based on psychological considerations. Several authors list a number of perceptual domains in which motor events are thought to play a direct role in the perception of certain properties. (**Haber, Ebenholtz, Wallach,** and **Welch** provide a systematic overview.) An example of such a property is position constancy, discussed by Wallach. There is general agreement among these commentators (with the exception of Haber, who appears open on the question) that this constancy occurs because perceivers are able to discriminate environmental displacement caused by their own movement from those caused by movement on the part of the environment. **Vonèche** proposes a new experiment in this connection which, he thinks, would allow a refined test of the von Holst theory underlying the explanation of many of the above phenomena. It is essentially aimed at ascertaining whether organisms make the crucial distinction, assumed by von Holst's theory, between environmental movements and self-movement, or whether all movement is always interpreted as self-movement, as claimed by Gibson's theory.

To be sure, Gibson (1966 *op. cit.*) has attempted to show how some of these discriminations could be made on the basis of input from the optic array alone, including visual input produced by S's movements and input derived from S's perception of parts of his own body. This will be considered in detail in 1.21. However, as **Shebilske** notes, the perception of direction has been shown to be accurate without visibility of body parts and without the availability of those structural overlaps of successively-visible portions of the optic array upon which Gibson's theory is based. That is, direction perception is available to a stationary observer, suggesting that it may be based on the direction of gaze.

Additional evidence for position constancy and for the concomitant role played by motor events in the production of this constancy it cited by **Bridgeman.** He reviews the familiar case of pressing against the eyeball with a finger and seeing the environment move in a direction opposite to the passive rotation of the eyeball. To this demonstration Bridgeman adds his own experiment, in which the eye fixates a point in space while being displaced by a finger. In this case the eye does not move, but the envrironment is seen as moving in the same direction as that in which the finger presses. Bridgeman points out that there is in this instance no Gibsonian relative-movement cue, as there would be in a tracking test, from which S could glean information about direction of movement. The only events that can explain the resultant perception are motor: the extraocular muscles must resist the pressure of the finger in a direction opposite to that induced by the finger. Thus, he argues, muscle innervation explains the perception.

1.13. Supportive comments based on neurophysiological considerations. Murthy discusses the role of the reticular formation in modulating impulses from both the ganglion cells in the retina, and the stretch receptors in muscle spindles. He thus points to the existence in the CNS of integrated centrifugal control of more peripheral sensory and motor events. From this he adduces the reasonableness, or the likelihood, of concomitant and interconnected motor and sensory processes as a widely applicable principle in visual perception [see also Roland: "Sensory Feedback to the Cerebral Cortex During Voluntary Movement in Man" *BBS* 1(1) 1978].

Taking cognizance of the fact that higher centers in the CNS modulate sensory and motor activity in concert, **Murthy** suggests a modification of von Holst's *reafferenzprinzip.* Murthy's conclusions about brain organization, it seems to us, were at least implied in the theories of von Holst, Sperry, and Teuber, and they were explicitly assumed in the work of Festinger, Burnham, Ono, & Bamber (1967 *op. cit.*) when these authors argue that *perceptual readiness,* rather than actual sensorimotor activity, is adequate for perceptual adaptation. Arguments similar to Murthy's have also been advanced by Konorski (1967 *op. cit.*) and Pribram (1971), among others.

Other evidence from neurophysiology is contributed by **Henn.** Agreeing in general with **Murthy** on the essential impossiblity of separating purely sensory and purely motor processes in brain, Henn considers as "strange" the question asked by many psychologists in

adaptation research — namely, whether organisms are able to monitor their own motor behavior at a central level. "Certainly," is Henn's response, citing as an example eye-movement signals recorded centrally 100 msec before the movements occur. He proceeds to present various examples of motor paralysis that illustrate the presence of central motor factors in perception, and he cites cases of plasticity even in phylogenetically-older sensorimotor systems. The latter examples, which reveal the probable influence of efferent central activity in human behavior, are especially interesting in view of the hypothesis stated by **Freides** that phylogenetically-older efferent systems in humans get "buried" under phylogenetically-newer systems. The implication is that the effects of the operations of efference may be hard to ascertain experimentally. Judging from the evidence referred to by Henn, this is not so – at least not under conditions of certain abnormalities such as ocular paralysis. Nevertheless, Freides' suggestion to include psychophysiological measures of autonomically-mediated reactions such as EMG in adaptation research, in addition to behavioral ones, may be fruitful.

Comments by **Roland** add a few cautions as to how much is known from neurophysiology that would support Held's theory. As will also be mentioned in 1.21, he sugggests that there is at present no neurophysiological evidence for an efference copy.

Unfortunately, neither **Henn**, nor **Murthy**, nor **Roland** go into detail on such specialized topics as shape perception, about which there is a great deal of argument among psychologists. On the basis of evidence reported by Henn and Murthy, and to an extent by Roland, the question is not whether motor and sensory factors are directly related in perception, but whether there are unusual conditions (of learning, etc.) under which these factors become relatively independent. It needs no belaboring that most psychologists ask the question in reverse.

1.2. Comments critical of Held's position: 1.21. Direct visual perception as an alternative to motor theories of perception. References to, and possible support for, theories of direct visual perception as possible alternatives to theories that posit direct involvement of motor effects in the formation of percepts were made by **Haber**. However, a full-blown challenge comes from **Turvey**, who devotes a long commentary solely to this issue. As usual, the strong points of theories of direct visual perception – such as the search for optic-array invariants – shine strongly and clearly. Error intrudes when these invariants are accepted as absolutes, or when there is indifference to empirical findings from both psychology and neurophysiology that are *not* in accord with direct theories of visual perception. Nor does the stated abhorrence of "intimating unanalyzable internal interpreters" make sense, since it appears to presume that neurophysiology does not exist.

As to neurophysiology, one might refer to **Henn**'s and **Murthy**'s findings and their applications to perceptual theory by **Kelso**, to the effect that the central nervous system "knows about" motor responses before they occur, and that there is centrifugal modulation of both motor and sensory phenomena. This implies feedforward, attentional mechanisms (also suspected in data reported by **Walk** and **Paap**), and feedback between motor and sensory factors in perception. This in turn presumes something like a *comparator* process, in which internal representations ("copies?") are confronted with afferent visual input. True, the presumptions at this point appear to run ahead of the evidence, since **Roland** suggests that there is at present no direct neurophysiological evidence for efferent copies nor, one assumes, for comparators. However, many, including Roland, agree that there are CNS representations of specific voluntary motor activities – so, one might ask, why not of voluntary activities *and* their anticipated afferent effects?

What about *behavioral* studies and their contributions to the above questions? **Turvey** considers the study by von Holst & Mittelstaedt that dealt with these issues. In considering this study, Turvey has to get into the distinction between voluntary and involuntary movement in formulating his control rules. That is, he has to consider the state of the organism as well as the state of the optic array. This is doing something that no theorist of direct visual perception is happy to accept.

1.22. Basic problems with the notion of efference copy. Kelso attacks the general notion of efference copy as being low in theoretical power. He wants to replace the concept by a theory based on information discordance and attention. Citing scores of references, Kelso makes the point that efferent commands do not specify states of individual muscles but control feedforward processes. The function of these is to prepare organisms for impending motor output and for afference arising from such action – that is, presumably, for von Holst's *re-afference*. There is, says Kelso, efferent modulation of afference. But is all of this really fundamentally different from von Holst, or is it a modern update? We would venture to propose that it is the latter.

Kelso rightly stresses attention as important in adaptation processes. He reminds us, for example, that adaptation occurs in that modality which in re-arrangement studies is not exercised during exposure, and that when attention is left uncontrolled experimentally, vision dominates. But what is attention? Kelso argues that self-initiated movement may be a contributor to adaptation because it sensitizes the organism to pay attention. Thus attention appears to be hooked into the feedforward and efferent paradigm, for Kelso as it is for von Holst, as well as for Held and others using von Holst's theory.

1.23. Held's theory of motor-sensory feedback in perception is in principle incapable of explaining adaptation of position or shape. The issue of positional adaptation is broached by **Welch**. According to Welch (1974 *op. cit.*), it was originally advanced by Howard (1970, 1971), who is supposed to have argued that motor outflow controls amplitude, direction, and speed of limb movement but not position. However, a close reading of Howard (1970) suggests that the above is an incorrect interpretation of pertinent statements made by him. What Howard (1970) says is that, whereas the training received by Ss in several of Held's studies involved amplitude of arm movement, the pre- and post-tests administered to them involved positioning of the limb. The argument is not that outflow to the limb *per se* is unconcerned with position control, but that the outflows controlling the training and the test behaviors in Held's experiments were totally different. Thus the issue raised by Welch may be laid to rest. It might be mentioned in passing that Rashbass (1961) reports a definite outflow for position, at least in the case of the eye. Parenthetically, the idea that training and test conditions must be as similar as possible is also mentioned and expanded upon by **Kohler**.

1.24. Motor events do not play a direct role in shape adaptation. This rather important limitation to the applicability of motor-sensory feedback theory has been stated not only by **Craske**, **Day**, **Lappin**, **Mack**, **Miller**, and **Wallach**, but, to an extent, by Held (1968) himself. It is also of central concern to **Rock**, who is willing to at least entertain this propostion as a hypothesis.

Wallach's arguments deserve particular attention. His starting point is the well-known observation that experimental subjects, viewing a line through prism goggles while moving their heads, will see the line (whose shape is transformed) move around in the visual field in phase with their own head movements. Wallach proposes the insightful hypothesis that the visual system attributes environmental movements that covary with bodily movements to the latter source, since genuine environmental events do not covary with movement of the head. Therefore, according to Wallach, the above covariance signals a nonobjective perception to S, and this sets the stage for subsequent visual adaptation. When the process of adaptation starts, the role played by motor activity ceases, according to Wallach. Hence his claim that movements play no *direct* role in the formation of the perception of shape itself.

Wallach's hypothesis concerning the implications of the covariance of head movement and the movement of the stimulus vis-a-vis perceptual objectivity is interesting. Nonetheless, it leaves an important question unanswered – namely, which direction

subsequent visual adaptation will take. Is the visual system really unaided in this matter by motor information that might be available and germane? For example, is it totally inconsequential for the system to know that, when viewing an apparently curved line, the eye can retain fixation of each part of it if the head moves along a straight trajectory rather than the one suggested by the apparent curve of the line? In general, since a given apparent shape in re-arrangement studies can be the result of a potentially infinite number of "real" shapes, experimental subjects *have* to rely on auxiliary information such as that obtainable, say, from scanning the stimulus. We might add that in our own laboratory we have evidence (unpublished) that the *shape* of an eye-scan required to fixate prismatically-transformed contours strongly affects contour-shape judgments.

Also important to the issue of the direct participation or nonparticipation of motor factors in the formation of shape perception are the comments of **Miller** and of **Lappin**. Both base much of their argument on findings reported by Miller & Festinger (1977). Summary conclusions are that the shape adaptation that occurred during experiments simulating prism conditions was unrelated to oculomotor retraining. By this is meant that, while saccadic eye movements showed progressive and regular changes over five days of tests, successive adaptation measures showed a much more erratic developmental course. Moreover, Miller & Festinger report additional data from two experiments showing that two quite different (indeed, opposite) learned eye movements corresponded to essentially similar visual adaptation scores. However, if we read Miller & Festinger correctly, in both of the above experiments visual adaptation was at the chance level. From insignificant relationships and data, even if multiplied by two, no significant conclusions can be drawn.

Two considerations thus stand in the way of unhesitatingly using the above findings to support the hypothesis of the absence of a connection between motor factors and shape perception. 1) Few people would regard this connection, were it to exist, as very simple or one-to-one. While the motor learning itself may be easy (and Miller & Festinger show that it is), *sensorimotor* learning may be difficult. Is it surprising, then, to find a relatively erratic (though in the aggregate somewhat consistent) process? 2) The second point to keep in mind is a finding obtained by Miller & Festinger, contrary to the overall conclusion: There was a highly significant connection between ease of motor learning and amount of visual shape adaptation in cases where easy movements were contrasted with difficult ones – surely not a finding in support of a hypothesis of total independence between sensory and motor processes.

Paap suggests that shape adaptation is a complex instance of direction adaptation, and that it may be especially hard to produce because the adaptation of numerous locations integrated over time is required.

Held's own view on the matter (Held 1968) must also be cited. Noting the relatively limited extent to which shape perception appears to be subject to adaptation in re-arrangement experiments, he proposed that limits to shape adaptation might be set by the so-called straight-line and curvature detectors that investigators such as Hubel & Wiesel (1965) claim to have found in various animals. This would be a cogent hypothesis if one were to accept the Hubel & Wiesel detectors as templates for the determination of absolute orientation and shape. However, as has been proposed by Caelli (1977), Hoffman (1966), Uttal (1973), and many others, there is much more to pattern analysis than is apparent from a template point of view. For example, both Caelli and Hoffman suggest that cortical cells extract differential information (in the mathematical sense) from impulses from retinal ganglion cells. In so doing, holistic (as opposed to local) characteristics of shape are computed as algebraic derivatives. Under such conceptions of shape the absolute nature of local features of a pattern are far less important than the differences between local features under internally- or externally-produced transformations. For example, what would be important about straightness on such a view would not be the absolute shape of a straight contour, or the firing of specific detectors, but whether cells responsive to similar orientations were fired successively under a scan of a contour, whether parts of the line translated across the retina at a constant rate, and so forth. Thus *relations* between successive cells, rather than the absolute response of each, become important. On premises such as these about shape perception, Held's remarks about the limits of adaptation to shape based on a template conception become irrelevant. Shape perception might, in fact, be extremely plastic, as is implied, for example, in Rock's (1966 *op. cit.*) remark that fitting a newborn with prism goggles might not result in any perceptual dislocations whatever.

1.25. Motor events have no direct perceptual role in rich visual environments; it is hence doubtful whether such events should be considered in perceptual theory at all. The proponent of this view, or one very close to it, is **Haber**. It is true that, as he claims, many of the re-arrangement studies have been done under relatively impoverished visual conditions. This is not the case, however, in the studies by Kohler (1964) nor in some better-controlled studies such as those by Held and his colleagues, whose subjects locomoted through hallways both actively and passively. **Riesen**'s observations, obtained under normal visual conditions, also go counter to Haber's generalization. One of Riesen's observations concerns the illusion of speeding up in an automobile when one steps on a nonoperative brake. The illusion obtains in spite of contradictory input from the optic array. Many more exceptions could be cited.

Haber adds that, even under the visually-impoverished experimental conditions of most visual re-arrangement studies, the motor parameters are the ones that normally adapt, whereas vision does not. Hence the claim that observed motor contributions to perceptual phenomena are excessively weak and can be eliminated from perceptual theory without great loss. Clearly, Haber's statements should be of concern to all who would like to understand whether and how motor events participate in perception. From the full range of phenomena discussed in this paper and the literature as a whole, the question that motor events participate directly in at least some perceptual events under some conditions cannot at this point really be ruled out. Even on the assumption that the direct involvement of motor events is normally extremely limited and weak, the problem of how this involvement is accomplished constitutes an exceedingly challenging theoretical (and possibly clinical) problem. Neither neurophysiology, as we understand it, nor psychological experimentation rule out a direct motor contribution to perception. Much work remains to be done to explore the whens and the hows.

1.26. The role of hysteresis in adaptation. The issue of hysteresis is mentioned by **Ebenholtz** and **Shebilske** and harks back to some studies by these authors and others, including a recent one by Willey, Gyr, & Henry (1978). In these studies, most of which contrast situations favoring central recalibration or potentiation, it is shown that visual adaptation to the re-arrangement of spatial location is due to hysteresis (muscle potentiation) rather than sensory-motor recalibration. Muscle potentiation is a peripheral effect and involves an involuntary and unconscious component of innervation to the eye muscle induced by sustained offcenter eye position such as occurs when one wears displacing prisms and, say, walks down a hallway. The continuous, unconscious innervation to the eye muscles during the post-test makes subjects look further to the right or left (depending on prism orientation during training) and induces the adaptation effects.

It is clear that the research on hysteresis has introduced a new parameter into adaptation research. However, it is not evident that the hysteresis principle can explain all observed adaptation effects. For example, in the case of adaptation to re-arrangement of shape, in which no motor activity is allowed in either the pre- or the post-test, potentiation can hardly have had an effect. The same should be true, even for adaptation to re-arrangement of location, if pre- and post-tests were to include tests of motor systems other than those involved during training. Finally, it has been shown in experiments

on adaptation to re-arrangement of size and depth by Wallach, Fry, and Bode (1972) and by Wallach & Halperin (1977) that not all their results are interpretable in terms of hysteresis.

2. Experimental factors favoring adaption in H & R type adaptation experiments

2.1. On the possible independence of motor and sensory events in the visual system. It may be recalled that we proposed in the conclusion section of our target paper that a possible reason for our negative results may have been that our experimental subjects decided to "live with," rather than confront, the conflict between visual-sensory and motor information. The fact that this may occur is neatly demonstrated in research reported by Bridgeman & Lewis (1976). Their findings suggest that while Ss, do not suffer from any spatial disorientation after making large saccades, and can point accurately to a target that had been displaced 2° during a saccade, tests performed while the saccade was in progress demonstrate that Ss were not consciously aware of the displacement. Bridgeman & Lewis conclude that visual information about position can enter the visuomotor system without influencing the cognitive system. This kind of effect deserves further study, since it could clearly be responsible for negative results in adaptation experiments in which motor and visual sensory information is confronted.

2.2. The requirement of explicit attention to contour in shape adaptation. Burnham explicitly raises the question of the conditions that will produce adaptation. He proposes the requirement of specific attention to contour during movement and sees this principle violated in the H & R experiment and in our replication. Our own comments (and **Day**'s) about the complexity of attending to the displacement of *specific* dots in a random dot environment are in line with Burnham's critique. In these latter studies it is of course not so much contour but the spatial displacement of the dots that is systematically transformed.

It would appear that **Burnham**'s maximally-adaptive subjects were in a situation analogous to our own (and H & R's), except for the important difference of having to "aim" at specific points and of having to make "blind" responses (i.e. in the absence of close sensorimotor feedback). Perhaps the latter is the requisite condition in order to skirt the problem of the independence between motor and visual sensory processes alluded to by **Bridgeman**.

2.3. The role of simultaneous eye and head movements in prism adaptation. Ebenholtz raises a point concerning the information that is available when both eye and head movements are encouraged in subjects, inasmuch as the visual feedback due to eye movements when one is wearing goggles is normal, while that due to head movements is not. He proposes the hypothesis that adaptation resulting from an H & R paradigm will be maximal when both eye and head movements are involved.

Finke proposes that head movement could be used as a variable in the H & R paradigm. Noting the absence of explicit instructions to Ss not to look at their bodies, **Redding** raises the possibility that, viewing their bodies while walking around inside the cylinder, Ss may have undergone proprioceptive adaptation which, in turn, could have eliminated any visual adaptation effects. This is undoubtedly a potentially cogent observation. We can only say that, having acted as experimental pretest subjects ourselves, we were never tempted to regard our own movements. This was in part because viewing the walls of the cylinder somehow helped to orient one while walking around in such relatively strange surroundings; also, and perhaps more importantly, the limited aperture afforded by the prism would have made self-viewing awkward in the extreme. It is not clear that there were any controls that kept H & R's subjects from disobeying the instruction not to look at themselves, thus leaving open the possibility that they behaved essentially identically to our own subjects.

2.4 Considerations about spatial frequencies. Steinbach, starting from the strong effect that spatial frequency has on pattern perception, raises the point that both the training stimulus (array of random dots) and the test stimulus (grid of parallel lines) in the H & R study have strong spatial-frequency characteristics. He asks whether the reason why the replication of the H & R experiment produced negative results, while the original experiment did not, might not be that, by pure chance, the spatial-frequency characteristics of the training and test stimuli in the H & R study were much more alike than those in our replication?

The above is certainly a novel, though not a very likely, possibility (i.e., what is the range of possible spatial frequencies from which either study could have chosen?). Probability aside, one might ask which specific hypothesis *Steinbach* has in mind: that curves were actually seen by Ss walking around in an environment specifically designed to eliminate the perception of contours, and that there was a neuronal adaptation after-effect that carried over to the viewing of a straight line grid? Are such curvature adaptation effects known to occur? (We are only familiar with threshold elevation, percieved frequency, and tilt after-effects.)

Even if *Steinbach's* hypothesis of such a powerful effect due to differences in spatial frequencies were pertinent to both studies, one wonders how the subjects in the H & R study escaped this effect during the passive phase, especially when many of them had passed through the same supposedly powerfully-effective visual stimulus field previously during the active condition. Nonetheless, on theoretical grounds, it may well behoove experimenters in adaptation research to pay attention to the dimension of spatial frequency. A similar point is raised by **Finke.**

2.5. Absence of shape-relevant information with base-right/base-left prisms under transformations produced by walking. Craske went to the trouble of partially replicating the H & R training conditions for himself. He notes that the flow of images over the retina was orthogonal to the stripes later used to test for adaptation, and thus that movement did not produce stimulation that was at all relevant to the subsequently perceived change in the straightness of verticals. Craske also notes that wearing either base-right or base-up prisms made the cylinder look curved. He proposes that this, via the Gibson effect, could have led to adaptation. Perhaps. Why it might have done so for H & R and not for us is, of course not explained.

2.6. Density of the stimulus. Mikaelian mentions the possibly important point of a higher dot density in the H & R study. The actual density used was not reported in the H & R study, nor was it specified in subsequent private correspondence between the present authors and Held. As Mikaelian informs us, it was reported in another reference. The greater density in H & R could conceivably have led to more information, although we still feel, with **Craske** and others, that the information available was not maximally relevant to contour, or was far too complex to attend to. Craske, in fact, informally used an array approximately as dense as H & R's without observing effects required to make H & R's hypothesis work. However, it would have been useful to use an identical stimulus in our replication.

2.7. Testing whether the experimental procedure is effective for a nonrandom stimulus. Finke raises the interesting point that trying out the experimental procedure in a cylinder that does contain apparent straight-line contours would allow for a check on the adequacy of the procedure. This suggestion, of course, is valid for both the H & R study and our replication.

3. Conclusions

Harvey wants to see a more precisely stated adaptation theory on our part, and presumably on the part of other theorists as well. To him, this tends to mean that kind of precision that is present in models of

artificial intelligence. Many, if not most, models of artificial intelligence, however, tend to be special-purpose models. To specify general models for sensorimotor perception that include – without undue simplifications – a wide variety of perceptual constructs and sensorimotor systems would be an enormous task. Thanks to many of the commentaries that have been made, including Harvey's, some of the logical, psychological, and neurophysiological reasons for motor–sensory feedback in perception have at least been stated more or less exhaustively.

It would seem that in some perceptual phenomena – e.g. position constancy, direction, distance, movement – motor events play a direct role, at least under some conditions. With respect to other perceptual phenomena such as shape, many researchers have serious reservations as to the direct involvement of motor processes. Nevertheless, it can be argued that the question is still very much open. It has been shown that some of the theoretical arguments against such direct involvement are subject to criticism; moreover, there exist some supportive experimental findings. The fact that, so far, shape- adaptation effects appear to be minimal makes sense in terms of the positional relearning that probably accompanies them. Moreover, the meaning of the limited degree of shape adaptation in re-arrangement studies also needs to be experimentally re-examined in view of the possible and paradoxical independence that may exist between "perceptual consciousness" and motor-sensory processes (**Bridgeman**; see also Roland: "Sensory Feedback to the Cerebral Cortex During Voluntary Movement in Man" *BBS* 1(1) 1978). On all these questions much important research remains to be done. Similarly, the question of perceptual plasticity to re-arrangement in newborn organisms (**Rock**), and the question of the conditions under which purely Gibsonian parameters of the optic array control perception (**Haber**) – or, conversely, when it is that motor parameters play a larger role – would seem worthy of further research. All these amount to a test of the limits of Gibson's theory of direct visual perception – not, as **Harvey** seems to imply, a full retreat from a broader sensorimotor theory when that theory appears to be in trouble. It may of course be that both theories need to be extensively modified.

We owe to **Freides** a delineation of the wider behavioral areas in which the role of motor factors in perception may be germane. He lists, among others, field-dependence, schizophrenia, certain learning disabilities, problems involving a coupling between vestibular and thought problems, signal detection, and so forth. Suggestions of this kind should stimulate interest in expanding the search for sensorimotor processes in perception.

On the issue of how positive results could be obtained in the case of the H & R paradigm, the findings reported by **Burnham** do not offer much encouragement. His findings would suggest that adaptation occurs only under a very stringent set of conditions – far more stringent than the conditions imposed in the H & R study and in our own attempted replication. How such strong positive results were obtained in the former study still seems to be shrouded in mystery. Only a detailed further study, along the lines indicated in our paper and incorporating the ideas present in **Burnham** and **Bridgeman's** work, would appear to offer some hope of resolving the riddle.

The hypothesis that motor events participate directly in the perceptual process thus appears to be partially supported by the evidence at this point. Is this hypothesis important enough to warrant further research, or is it the case, as is more or less implied in **Haber's** commentary, that the hypothesis explains very little in terms of everyday perceptual processes? It is argued here that the hypothesis is crucially important to provide a model with an *integrated* concept of attention, expectation, or feedforward, as well as a concept of sensitivity on the other. Gibson (1963, p. 12) himself formulated the central task for perceptual theory as follows: "We had to suppose that the role of the senses, their sole function, was not to yield sensations. Instead of receptors, i.e. receivers and transducers of energy, they appear to be systems for exploring, selecting, and searching ambient energy. . . . *This new picture of the senses includes attention as part of sensitivity, not as an act of the mind upon the deliverances of the senses*" (emphasis added). In spite of this program, Gibson seems vague about the determinants of attention, referring, for example, to areas of "high information" and of "movement" in an optic array as "attention-getting." These principles are ad hoc and, as pointed out by Mace & Pittenger (1975), independent of the theory of perception. It would appear that attention, expectation, and feedforward processes are far more integrated with the process of perception itself in the theories of von Holst, Sperry, Held, Kelso, and others. The latter, in effect, constitute the theoretical standard-bearers of the basic program for perception that was so well formulated by Gibson. Needless to say, the exploration of the precise nature of attentional processes along lines that include the sensorimotor nature of perception has only begun. We fully agree that some of the old lines of attack on these problems should be abandoned in favor of new approaches, of which a good many candidates have been brought forward in this Commentary.

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